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Climate Change and Insect Pests

EDITED BY **CHRISTER BJÖRKMAN** AND **PEKKA NIEMELÄ**

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Climate Change and Insect Pests

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Climate Change and Insect Pests

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De brister tidigare och tidigare, isarna
Säkert! (Annika Norlin)

Foreword

As this book goes to press in September 2015, the average atmospheric CO_2 on Planet Earth has just surpassed 400 ppm. The timing was a remarkably good match with predictions from the very first report of the Intergovernmental Panel on Climate Change in 1990 (400 ppm in 2015 matches 'scenario c', based on constant rate of anthropogenic CO_2 production). Over the same 25-year interval, mean global air temperature increased by ~0.3°C, which was also a good match with IPCC predictions from 1990. What could not be predicted then, even in qualitative terms, was what these atmospheric changes would mean to biological populations and communities. Indeed, it was reasonable to question whether these changes would have more than occasional subtle effects on ecological systems. After all, most of us would never notice if the temperature of the room where we sit changed by 0.3°C. This book is a testimony to how much we have learned – especially in the last few years – about the response of biological populations to the changing atmosphere of Planet Earth, and the consequences for human interactions with ecosystems.

The title of the book is 'Climate Change and Insect Pests', but the implications extend well beyond these topics. Insect pests provide an excellent framework for evaluating climatic effects on a wide range of ecological systems because pest species tend to be particularly well studied in terms of taxonomy, physiology, geographic distributions, population dynamics, species interactions and ecosystem function. Furthermore, insect pests are conduits for transferring ecological changes to human society. Thus the reviews, syntheses, models and projections offered within this volume provide a starting point for anticipating when and how ecological systems will change under future climates.

The book clarifies that a prominent emerging challenge for ecology and natural resource management is predicting which biological systems will be sensitive versus stable in the face of continuing climate change. One conclusion is that climatic effects on insect pestilence are real and are happening now. For example, millions of hectares of boreal forest are being dramatically altered by recent poleward expansions of bark beetles and defoliators that have been permitted by climate warming (e.g. see chapters by Raffa *et al*., Økland *et al*. and Ammunét *et al*.). On the other hand (Battisti and Larsson), these clear examples involve only a few species from within even fewer clades, and many populations of insect pests have been relatively stable in terms of distributions and dynamics. This intellectual quest takes readers to frontiers of contemporary ecological research that include: connecting niche theory and physiology in species distribution models (Hill and Thomson); effects of climatic variation on plant–herbivore interactions (Julkunen-Tiitto *et al*., Neuvonen and Virtanen); the evolutionary ecology of plant–herbivore interactions under rapid environmental change (Rasmann and Pellissier); thermal sensitivity of top-down controls by enemies of plant pests (Kalinkat and Rall, Eigenbrode *et al*.); and climatic effects on more complex plant–pest interaction systems, such as the frequent cases involving symbioses between plant pathogens and insect vectors (Roques *et al*.). A highlight of the book is consideration of climatic effects on agricultural pests (including Terblanche *et al*., and Lindström and Lehmann), which have been less studied in this regard than forest pests. In fact, this book is the first I know of to consider climatic effects on plant–pest interactions with a scope that runs from intensively managed, short rotation, agricultural systems to unmanaged, slow-growing forests.

As the book illustrates, our deep knowledge of the biology of plant pests makes them a convenient model for considering climatic effects on biological systems in general, but we should also remember that we have good knowledge of plant pests because they matter so much to us. Since the beginning of recorded history, plant production systems all over the world have been subject to episodic, sometimes catastrophic, failures due to outbreaks of pests. The relevance of plant pests to global society grows as human population grows. Our need for ecosystem services has grown by about 2 billion humans since the first IPCC report in 1990. Similar to the case of predicting atmospheric CO_2 25 years ago, it seems we have pretty good models for anticipating effects of climate change on plant production systems in the absence of pest outbreaks (e.g. within IPCC AR5). However, understanding climatic effects on pest populations has additional layers of complexity due to the importance of species interactions and feedbacks in the population dynamics. From this book we know that the risks of pest outbreaks are increasing in some ecosystems, stable in others, and probably decreasing in some. This uncertainty from changing risks of plant pestilence is a leading challenge to the stability of food and fiber production systems in the 21st century. This book charts a course for reducing uncertainty regarding pests – and therefore increasing environmental security for human societies – through the application of good science, general theory, and strong linkages between science and management (Björkman *et al*.).

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16 May 2015

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Climate Change and Insect Pest Distribution Range

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Abstract

There is a pressing need to understand better the dynamics of species' distribution, in particular when it comes to predicting the outcomes of climate change-inflicted variations in the range distributions of insect pests. Several insect life history traits, such as survival, growth rate and voltinism, are likely to change in a warmer environment, and it is to be expected that at least some changes will contribute to altered range edges. For many insect taxa, range expansions are not easy to detect, simply because their presence remains undetected in habitats at range edges, where they are likely to occur at low densities. Insect pests are a group for which information on range expansion is beginning to accumulate, for the obvious reason that their effects on managed ecosystems often require action. Thus, increasingly managers of agriculture and forestry are concerned with the predicted range expansions of important insect pests.

This chapter offers an update on the range expansions of insect pests in agriculture and forestry, native and alien. We summarize information from the literature where climate change has been interpreted as, or predicted to become, the driver of range expansion. We discuss the type of evidence for the expansion, ongoing or predicted to occur, and aim to classify according to its empirical nature.

A critical read of the database of the literature on climate change resulted in surprisingly few documented examples of climate change-induced range expansion. Of course, long-term trends in the distribution and abundance of insect pests are notoriously difficult to document. Thus, it is possible that more insect pests could have responded to climate change, or are likely to do so in the near future, than can be detected in our literature search. It is also possible, however, that biological systems, including insect pests, are less sensitive to direct climate effects than previously thought (due to the buffering effects of trophic interactions). Future research needs to focus more on the mechanisms of responses to changed climate in order to understand better, and predict more accurately, the likelihood that insect pests will expand their outbreak range.

1.1 Introduction

The geographical distribution of organisms is, in principle, easy to define; namely, the area under which, at any given point, population growth is positive (e.g. Gaston, 2003). Unfortunately, in practice, species distribution areas are difficult to determine in any detail; in fact, Gaston (2009) argues that for no single species do we have a complete understanding of its distribution. Despite

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these obvious difficulties, there is a pressing need to understand better the dynamics of species' distribution, in particular when it comes to predicting the outcomes of climate change-inflicted variations in range distributions.

Insects are highly sensitive to increases in temperature because of their ectothermic lifestyle, in particular species inhabiting high-latitude environments (Deutsch *et al*., 2008). Several life history traits, such as survival, growth rate and voltinism, are likely to change in a warmer environment. Thus, even though we are far from understanding the details in range expansion dynamics, we would still expect climate-induced changes in life history traits to result in altered range edges under certain circumstances. Research over the past three decades has shown convincingly that such range shifts have indeed occurred for a number of taxa, with respect to latitude as well as elevation (Parmesan and Yohe, 2003; Chen *et al*., 2011).

For many insect taxa, range expansions are not easy to detect, simply because their presence remains undetected in habitats at the range edge, where they are likely to occur at low densities. It is not surprising, therefore, that our best understanding of range expansion following warming refers to taxa that are particularly conspicuous and of special interest to collectors, such as Lepidoptera (e.g. Mair *et al*., 2012). Economically important species ('pests') is another group for which information on range expansion is beginning to accumulate, for the obvious reason that their effects on managed ecosystems often require action. Thus, managers of agriculture and forestry increasingly are concerned with the predicted range expansions of important insect pests (e.g. Weed *et al*., 2013). In addition, accidental introductions of insects into novel geographic areas where they subsequently acquire pest status, i.e. become invasive (Blackburn *et al*., 2011), have increased in numbers during the last decades, and at least partly because of changes in climate (e.g. Robinet and Roques, 2010).

This chapter offers an update on the range expansions of insect pests in agriculture and forestry, native and alien. We summarize information from the literature where climate change has been interpreted as, or predicted to become, the driver of range expansion. We discuss the type of evidence for the expansion, ongoing or predicted to occur, and aim to classify according to its empirical nature.

1.2 Concepts and Definitions

In recent decades, much has been said about climate warming and increasing threats from insect pests to forestry and agriculture. In a very general way, such claims seem to be based on good logic; weather, and in particular temperature, does have a strong impact on insect growth and survival. However, a fair amount of these claims lack scientific support. It should be remembered that almost all insect populations are part of organism communities where trophic interactions play a crucial role. This means that extrapolating from climate-induced effects on insect individuals, or populations in isolation, to real insect populations in complex food webs must be viewed with caution.

Here, we present the state-of-the-art when it comes to understanding climate change-induced range expansion; intensified dispersal to novel geographic areas is an expected consequence of climate change. It is notoriously difficult to obtain good data on the dynamics of the distribution range of insects because of the large spatial scale, the timescale over which range changes take place and the difficulty in observing insect individuals (often at low density) that have extended outside of their previous range. The complex spatio-temporal dynamics taking place at the range edge (latitudinal and elevational) in need of consideration when determining insect range expansion are outlined schematically in Fig. 1.1.

Our interest here is on the range expansion of insect pests in forestry and agriculture, i.e. insect populations that occur at densities high enough to cause economic damage. This type of insect is likely to be discovered by managers, and scientifically reported by applied entomologists, at the

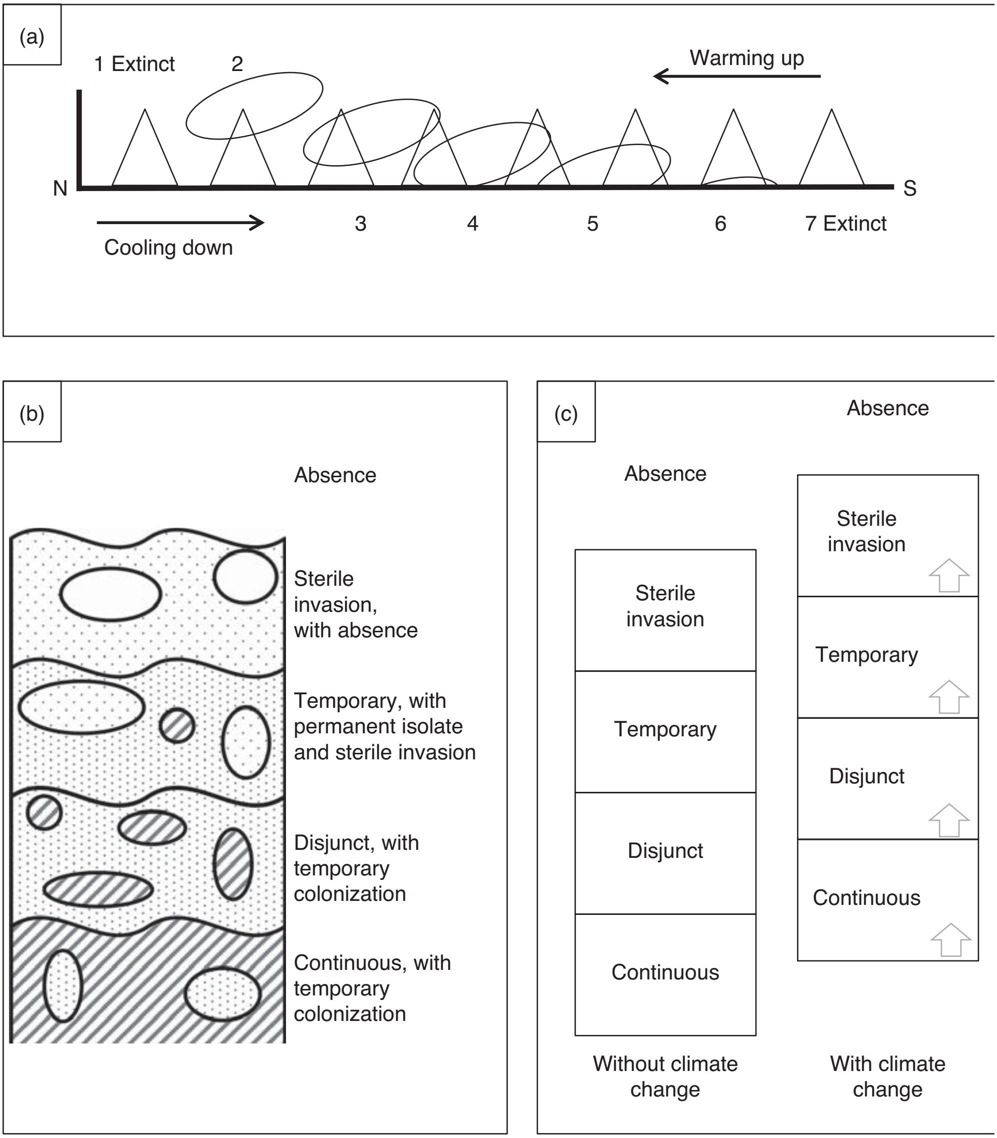

Fig. 1.1. Schematic representation of the dynamics of distribution range and effects of changes in climate. (a) Effects of changing climate on the distribution of organisms in the northern hemisphere (modified from Gorodkov, 1985). The horizontal axis represents the latitude and the vertical axis the elevation. The triangles along the horizontal line identify mountains occurring at different latitudes. The oblique lenses represent the potential range of the organism as determined by climate (both inclination and width of the lens may vary depending on the reaction norms of the individual species). The potential range may shift from south to north and from low to high elevation, and vice versa, depending on warming and cooling of the climate. Gorodkov exemplified different types of distribution that could be observed in relation to the position of the lens along the gradient, i.e. 2: montane local (endemic), 3: montane wide, 4: disjuncted plain–montane, 5: continuous plain–montane, 6: plain local (endemic). Types 1 and 7 drive to extinction. Types 4 and 5 are the most common and are associated with wider geographic distribution. (b) Spatial dynamics of hypothetical populations at the range edge (modified from Gorodkov, 1986). (c) Expected effects of climate change on the spatial occurrence of populations as detailed in b.

early stage of an expansion (a 'true' expansion, however, might have taken place earlier through the dispersal of pioneer insects that have remained undetected). Consequently, this means that the literature is likely to cover most of the insect pests that have expanded into novel areas. For the purpose of this chapter, we compiled a database on pest expansion by conducting keyword searches using Web of Science and by examining the literature-cited sections of the papers.

When putting together the database, we discovered very soon that the quality of the empirical support for range expansion varied substantially among publications. We classified publications reporting evidence of climate change-induced range expansion into three categories: (i) studies where recent expansion has been observed and documented, and where there are plausible causal explanations linking expansion to climate change; (ii) studies documenting recent changes in range distribution possibly associated with climate change, but with little or no mechanistic support; and (iii) studies reporting the outcomes of modelling attempts, most often in the form of species distribution models (also referred to as envelope models), with the primary aim of predicting future changes in species ranges but with little or no evidence of actual range change occurring.

One could perhaps argue that it is only the first category that presents evidence allowing conclusions about causal relationships between climate change and range expansion. For the other two categories of studies, firm conclusions about the role of climate change are more problematic. In particular, results from the third category, envelope modelling, have commonly been discussed despite the fact that the approach is entirely correlative, resting on past and expected future relationships between spatial variation in climate and species occurrence. Thus, envelope models allow predictions about potential future distributions, but whether or not these will be realized depends on a number of unknown conditions, in particular novel trophic interactions.

1.3 Database

The literature survey resulted in 50 species whose range have been observed to be affected by climate change, or predicted to be so in the future (Table 1.1). The number of species with observed range expansion and with a plausible causal explanation (Category 1) was, however, much smaller (eight cases). For 17 species, range expansions have been documented, but without clear empirical support for the hypothesized link to climate change (Category 2). For the remaining 25 species, range expansions were predicted based on modelling data (Category 3), either climate matching alone or climate matching combined with insect physiology data. Cases refer mainly to pests from the temperate and boreal region.

Category 1 includes seven forestry pests and only one agricultural pest. There are six native and two alien species. A latitudinal range expansion was observed in all species, while elevational and longitudinal expansions were also observed in four and one species, respectively. The most frequent mechanism of range expansion is reduced winter mortality in the novel areas. In the following, we summarize first the key findings for the Category 1 species, starting with the most known examples of native forest defoliating moths and bark beetles, and then proceed with other native and alien species in forestry and agriculture.

The pine processionary moth (*Thaumetopoea pityocampa*) is one of the best examples of an insect responding to climate change, documented in a number of publications during recent years (e.g. Battisti *et al*., 2005; Buffo *et al*., 2007; Robinet *et al*., 2007, 2013). Increased winter temperature results in better performance of the winter-feeding larvae. The improved performance comes from the combined effect of night temperature permissive of feeding (T > 0°C) and day temperature allowing food digestion when the larvae rest in the tent (T > +9°C). The high day temperature is made possible through exposure of the larval tents to solar radiation, even when air temperature is far below the threshold of +9°C (Battisti *et al*., 2005). The improved larval performance has

Table 1.1. Range expansion of insect pests in agriculture and forestry.

Category	System	Origin	Species	Host	Expansion	Area	References
1. Range expansion observed and mechanism known	Forestry	Native	*Dendroctonus frontalis*	Pinus	LA	N America	Ungerer *et al*., 1999; Trân *et al*., 2007
			Dendroctonus ponderosae	Pinus spp.	E, LA, LO	N America	de la Giroday *et al*., 2012; Raffa *et al*., 2013
			Dendroctonus rufipennis	Picea	LA	N America	Berg *et al*., 2006; DeRose *et al*., 2013
			Epirrita autumnata	Broadleaves	E, LA	Europe	Jepsen *et al*., 2008; Ammunét *et al*., 2012
			Operophtera brumata	Broadleaves	E, LA	Europe	Jepsen *et al*., 2008; Ammunét *et al*., 2012
			Thaumetopoea pityocampa	Pinus, Cedrus	E, LA	Europe	Battisti *et al*., 2005; Robinet *et al*., 2007
		Alien	*Adelge stsugae*	Tsuga	LA	N America	Paradis *et al*., 2008; Fitzpatrick *et al*., 2012
	Agriculture	Alien	*Nezara viridula*	Various	LA	Japan	Musolin and Saulich, 2012; Tougou *et al*., 2009
2. Range expansion observed and mechanism unknown	Forestry	Native	*Malacosoma disstria*	Broadleaves	LA	N America	Dukes *et al*., 2009; Lapointe-Garant *et al*., 2010
			Matsucoccus feytaudi	Pinus	LO	Europe	Burban *et al*., 1999
			Neodiprion sertifer	Pinus	LA	Europe	Virtanen *et al*., 1996; Veteli *et al*., 2005
			Thaumetopoea processionea	Quercus	LA	Europe	Groenen and Meurisse, 2012; Meurisse *et al*., 2012
			Zeiraphera diniana	Larix, Picea	E	Europe	Esper *et al*., 2007; Johnson *et al*., 2010

continued

Table 1.1. *continued.*

Category	System	Origin	Species	Host	Expansion	Area	References
		Alien	*Agrilus planipennis*	Fraxinus	LA, LO	N America	Muirhead *et al.*, 2006
			Andricus spp.	Quercus	LA, LO	Europe	Walker *et al.*, 2002
			Anoplophora glabripennis	Broadleaves	LA, LO	China	Smith *et al.*, 2001; Bancroft and Smith, 2005
			Cameraria ohridella	Aesculus	LA, LO	Europe	Gilbert *et al.*, 2005
			Dryocosmus kuriphilus	Castanea	LA, LO	Europe	EFSA, 2010
			Lymantria dispar	Broadleaves	E, LA	N America	Liebhold *et al.*,1992; Régnière *et al.*, 2009
			Phyllonoricter platani	Platanus	LA, LO	Europe	Sefrova, 2001 in Gilbert *et al.*, 2005
			Thecodiplosis japonensis	Pinus	LA, LO	Korea	Lee *et al.*, 2007
	Agriculture	Native	*Diuraphis noxia*	Cereals	E, LA	China, EU, USA	Zhang *et al.*, 2012; Ulrichs and Hopper, 2008
			Heteroptera spp.	Rice	LA	Japan	Kiritani, 2013
			Schizaphis graminum	Cereals	LA	Europe	Harrington and Woiwod, 2007
		Alien	*Liriomyza huidobrensis*	Various	LA	Europe	Cannon, 1998
3. Range expansion predicted based on models	Forestry	Native	*Choristoneura fumiferana*	Abies, Picea	E, LA	N America	Candau and Fleming, 2011; Régnière *et al.*, 2012
			Dendroctonus rhizophagus	Pinus	E, LA	N America	Smith *et al.*, 2013
			Lymantria monacha	Conifers	LA	Europe	Vanhanen *et al.*, 2007
			Tomicus destruens	Pinus	E, LA	Europe	Horn *et al.*, 2012
			Tomicuspiniperda	Pinus	E, LA	Europe	Horn *et al.*, 2012
		Alien	*Corythucha ciliata*	Platanus	LA	China	Ju *et al.*, 2013

Agriculture	Native	*Chilo suppressalis*	Rice	LA	Japan	Morimoto *et al.*, 1998
		Conotrachelus nenuphar	Prunus	LA	USA	Ulrichs and Hopper, 2008
		Cydia pomonella	Malus	LA	Europe	Rafoss and Saethre 2003; Svobodová *et al.*, 2013
		Helicoverpa spp.	Various	LA, LO	Australia, USA	Zalucki and Furlong, 2005
		Helicoverpa zea	Various	LA, LO	USA	Ulrichs and Hopper, 2008
		Leptinotarsa decemlineata	Solanaceous	LA	EU, USA	Ulrichs and Hopper, 2008
		Lobesia botrana	Vitis	LA	Europe	Svobodová *et al.*, 2013
		Ostrinia nubilalis	Maize	LA	Europe, USA	Cannon, 1998; Svobodová *et al.*, 2013
		Plutella xylostella	Crucifers	LA	N America, Japan	Cannon, 1998; Morimoto *et al.*, 1998
		Rhopalosiphum padi	Cereals	LA	Europe	Svobodová *et al.*, 2013
		Sitobion avenae	Cereals	LA	Europe	Svobodová *et al.*, 2013
		Tribolium confusum	Flour	LA	Japan	Morimoto *et al.*, 1998
	Alien	*Bactrocera oleae*	Olea	LA	USA	Gutierrez *et al.*, 2009
		Ephestia kuhniella	Flour	LA	Japan	Morimoto *et al.*, 1998
		Oulema melanopus	Cereals	LA	Europe	Svobodová *et al.*, 2013
		Pectinophora gossypiella	Cotton	LA	USA	Gutierrez *et al.*, 2006
		Phthorimaea operculella	Solanaceous	LA	World	Kroschel *et al.*, 2013
		Solenopsis invicta	Various	LA	USA	Ulrichs and Hopper, 2008
		Tetranychus evansi	Solanaceous	LA	World	Meynard *et al.*, 2013

Note: expansion type – E = elevational; LA = latitudinal; LO = longitudinal.

resulted in a progressive colonization of areas outside of the core range. Furthermore, moth mobility has also been found to be favoured by the increase in temperature; warmer summer nights allow a more frequent achievement of the flight threshold temperature (Battisti *et al*., 2006). In addition, human inadvertent translocation of the insect, likely as pupae in the soil of ornamental trees, has further contributed to the dispersal and has resulted in the establishment of populations outside of the historic range (Robinet *et al*., 2012, 2013). Novel host tree species encountered during the expansion are suitable for larval development (Stastny *et al*., 2006), and thus it seems likely that range expansion will continue as long as temperature will increase. At the southern edge of the distribution range, in northern Africa, *T. pityocampa* is expanding in native mountain stands of cedar (*Cedrus atlantica*), threatening these endangered ecosystems (Sbabdji and Kadik, 2011), while it remains stable in the low-elevation stands of Aleppo pine (*Pinus halepensis*) facing the Sahara desert (Zamoum and Démolin, 2005).

Bark beetles (*Dendroctonus* spp.) in North America have been discussed extensively in relation to climate change (e.g. Weed *et al*., 2013). Several *Dendroctonus* species have been proposed to be potential threats to forestry in novel areas (Bentz *et al*., 2010), but the mountain pine beetle, *Dendroctonus ponderosae*, is by far the best-studied one for which there is evidence of an ongoing expansion. It seems clear that increased temperatures have made it possible for the beetle to survive winter in geographical areas previously unsuitable; for example, expansion has been documented to occur in Canada, both northwards in British Columbia and westwards into Alberta (Carroll *et al*., 2006). The mountain pine beetle has also dispersed into higher mountainous areas not previously inhabited (Raffa *et al*., 2013). The expansions have been possible because potential host trees grow outside its historic range (Bentz *et al*., 2010). Outbreaks of the mountain pine beetle result in extensive tree mortality; the latest outbreak in central Canada has been of a magnitude not previously recorded, affecting more than 15 million hectares (Mha) of pine forests (mainly lodgepole pine, *Pinus contorta*) (Kurz *et al*., 2008). Predicted increased temperatures, leading to higher winter survival of larvae, are expected to enable expansion into areas historically not occupied, including boreal Canada, where a host shift to Jack pine, *Pinus banksiana*, seems likely to occur (Erbilgin *et al*., 2014). However, it is essential for the mountain pine beetle, and many other bark beetle species, to achieve synchronized population emergence in order to mass attack host trees successfully; modelling results indicate that as summer temperatures increase in potential novel areas (e.g. eastern USA), the timing of emergence could be disrupted, and thus affect population growth negatively and decrease the risk of outbreaks (Bentz *et al*., 2010).

The northward expansion of the southern pine beetle, *Dendroctonus frontalis*, has been linked to improved conditions for overwintering beetles, either larvae or adults, based on physiological threshold (lower lethal temperature) and climate predictions (Ungerer *et al*., 1999; Williams and Liebhold, 2002). The link between increased temperature and damage has been explored by Trân *et al*. (2007), resulting in a positive effect mainly in the northern expansion area, while the core populations do not seem to respond strongly to temperature variation. Waring *et al*. (2009) have developed a phenological model predicting more generations per year as a consequence of temperature increase, although it is not clear whether the change has resulted in more expansion or pestilence. Recently, Weed *et al*. (2013) reported range expansion in New Jersey, which is associated with the overcoming of thermal thresholds and with large damage to forest stands.

An elevational shift of the spruce bark beetle, *Dendroctonus ruficollis*, has been hypothesized in Engelmann spruce (*Picea engelmannii*) forests of north-central USA, based on a bioclimatic model (DeRose *et al*., 2013). Both winter and summer temperature increases seem able to promote population growth and expansion outside of the core range, although stand traits such as stand basal area and frequency of spruce trees can be as important as abiotic factors in affecting beetle performance. Berg *et al*. (2006) have shown that high summer temperatures are responsible for the outbreak range expansion of this species in Alaska and Yukon.

The autumnal moth (*Epirrita autumnata*) and the winter moth (*Operophtera brumata*) feeding on mountain birch (*Betula pubescens*), at the northern edge of their ranges in Scandinavia, have recently been reported to be affected by climate change (Jepsen *et al*., 2008). For both species, it has been shown that the outbreak range has shifted. *O. brumata* has experienced a pronounced north-eastern expansion into areas previously dominated by *E. autumnata* outbreaks, whereas the latter has expanded into the coldest, most continental areas. The hypothesized mechanism involves the increase in winter temperature, leading to higher survival of overwintering eggs (Jepsen *et al*., 2008).

There are two examples of climate change-induced range shifts among sucking insects. The hemlock woolly adelgid (*Adelges tsugae*) has extended its distribution range into north-eastern USA from the site of introduction in Virginia (Evans and Gregoire, 2007; Paradis *et al*., 2008). The limiting factor is winter temperature, which can be lethal for the overwintering stages (Paradis *et al*., 2008). With the increase in mean minimum winter temperature, the aphid has expanded progressively to the north and simultaneously built up high density in the already colonized areas, contributing greatly to hemlock dieback (Fitzpatrick *et al*., 2012). In this case, the temperature-dependent spreading occurs from the south to the north, leaving behind dead trees on which the insect cannot persist. The green stink bug (*Nezara viridula*) in Japan is progressively occupying areas located outside the historic northern edge of the range, because of more favourable winter temperature for the adults (Musolin and Saulich, 2012). Interestingly, the expansion has resulted in a displacement of a native bug of the same genus (*Nezara antennata*) (Tougou *et al*., 2009).

In Category 2, the forest pests are also predominant (13 species out of 17). Eight species are native and nine alien. Again, the latitudinal range expansion is the most common (15 species), alone or combined with elevational and longitudinal expansion. The most commonly suggested mechanisms refer to the effect of increased temperature on insect physiology. In several native species of defoliating and sap-sucking insects, an outbreak range expansion has been observed at the northern edge, whereas in other species, such as the larch bud moth, *Zeiraphera diniana* (Johnson *et al*., 2010), and the gypsy moth, *Lymantria dispar* (Liebhold *et al*., 1992; Régnière *et al*., 2009), the outbreak area has shifted to higher elevation. For alien species, a faster developmental rate has been observed in the emerald ash borer, *Agrilus planipennis* (Muirhead *et al*., 2006), a faster dispersal in the gall wasps (Walker *et al*., 2002; Gilioli *et al*., 2013) and in the Asian longhorn beetle, *Anoplophora glabripennis* (Smith *et al*., 2001; Bancroft and Smith, 2005), increased voltinism in leaf miners (Cannon, 1998; Gilbert *et al*., 2005) and better winter survival in pine gall midges (Lee *et al*., 2007).

In Category 3, the agricultural pests are more frequent (19 species out of 25). Seventeen species are native and eight are alien. Latitudinal range expansion is predicted for all species, and for some of them is combined with elevational and longitudinal expansion. All cases are based on the envelope model, but in three species there is a plausible link with insect physiology. Specifically, Régnière *et al.* (2012) predict a northern and upward shift of the outbreak area of the spruce budworm *Choristoneura fumiferana*, in North America, because of improved overwintering conditions for the larvae and the suitability of susceptible host plants. Gutierrez *et al*. (2006) predict that, with winter warming, the cumulative negative effect of low temperature on the diapausing larvae of the cotton bollworm would be lower, allowing a faster colonization of the Central Valley in California. Gutierrez *et al.* (2009), however, suggest that the range of the olive fly, *Bactrocera oleae*, will retract in the south and expand in the north part of the range, both in North America and in Europe, due to the effect on the adult flies of high temperature during summer and a milder winter, respectively. Based on the response of native *E. autumnata* and invasive *O. brumata* to winter temperature, Ammunét *et al*. (2012) predict the likely expansion of another birch geometrid species, *Agriopis aurantiaria*, which is currently more limited by temperature than the other geometrid species but could become invasive if conditions become more permissive. The sycamore lace bug, *Corythucha ciliata*, an invasive species in southern China, does not seem to be limited in its expansion to the south as long as the temperature is lower than 43°C, as shown by heat-shock treatments carried out in the laboratory on local genotypes (Ju *et al*., 2013). Finally, both cosmopolitan (*Helicoverpa armigera*) and local (*Helicoverpa punctigera*) corn earworms do respond well to weather fluctuations in Australia. Zalucki and Furlong (2005) relate the pheromone-trap catch with rainfall pattern in the area of origin, indicating that a change in climate associated with a change in the precipitation regime may affect the range occupied by migratory moths, although this can have a limited effect in time.

1.4 Discussion and Conclusions

The range edge is characterized by strong dynamics, as illustrated in Fig. 1.1. An expansion of the distribution range of an insect pest thus needs to be manifested as the permanent establishment outside of the area of historic distribution. It is not possible to come to any firm conclusions about permanent occupancy, unless the expansion of the range edge is sufficiently large. The cases that we list as evidence of real expansions (Category 1) seem to meet such a criterion. It might come as a surprise that we have not considered more than eight species to show climate change-induced range expansion. It has been implied that many more insect pests have expanded their range (referred to as Categories 2 and 3). It is possible that these species will indeed expand in the future, as predicted, but there is presently insufficient empirical support for this yet to have occurred. It is interesting that there are almost no signs of retraction of the distribution range of insect pests (at low latitudes and elevations), seemingly in contrast with other insect groups such as certain Lepidoptera (Thomas *et al*., 2006). Whether or not this is a real difference, and if so for what reason, is difficult to determine because little is known about retraction dynamics. We note, however, that the host plants of insect pests are managed by humans, sometimes intensively, and this could result in insect pests having a better chance to tolerate suboptimal weather conditions in the putative retraction area; for example, due to a surplus of habitats offering a variety of microclimates. A possible example is *T. pityocampa*, which is well established at its southern range in the large afforestation belt in front of the Sahara desert in southern Algeria (Zamoum and Démolin, 2005).

From a management point of view, it is of utmost importance to understand whether or not a range expansion of a particular insect pest will also lead to this insect becoming a pest in the novel area, and if so, whether the dynamics will be similar to that in the historic range (e.g. with respect to outbreak frequencies and magnitudes). Very little is known about this. Climate-induced range expansion in *T. pityocampa* is indeed associated with outbreaks in the newly colonized areas; however, the population dynamics seem to be determined more by endogenous than by exogenous (i.e. weather) factors (Tamburini *et al*., 2013). In spite of the evidence of outbreak range expansion by *O. brumata* at high latitudes (Jepsen *et al*., 2008), Tenow *et al*. (2013) have not found evidence of changed population dynamics (periodicity of travelling waves) of this geometrid across Europe during the past 60 years, a period with documented increases in temperature. The expansion of tree-killing insect species (e.g. mountain pine beetle) is an interesting special case because their activity often results in large areas of dead trees (Raffa *et al*., 2013), thus offering unsuitable habitats for future generations;

this can result in a further expansion simply because of lack of suitable resources.

Accidental introductions of non-native organisms (alien species) do not always lead to them being invasive (Tobin *et al*., 2011), i.e. becoming established as economically important pests (Blackburn *et al*., 2011). In cases where alien species do expand their distribution range from the point of introduction, their successful establishment is assumed to be favoured by changes in climate (e.g. Robinet and Roques, 2010). There are good reasons to suspect that climate change has contributed to insect species becoming invasive, although our database does not give unequivocal support for this suggestion; for example, we found no more than two species in Category 1. It will be interesting to see if alien species already established might colonize the colder parts of the potential habitat at the same rate, assuming that temperature might limit their performance. Because expansion rates associated with climate change are in the lower part of the interval available for accidentally introduced aliens (Liebhold and Tobin, 2008) and aliens released for weed control (Paynter and Bellgard, 2011), it seems likely that temperature is still limiting the expansion potential. We may thus predict that climate change will facilitate the further establishment of alien species in the potential habitat.

The range expansion of insect pests, and their associated outbreaks, includes two main features – population growth and dispersal. Thus, the source population in the historic range needs to have a density high enough in order for enough dispersing insects to leave the core area successfully, a recent example being the mountain pine beetle dispersing eastwards and northwards from its outbreak in central British Columbia (de la Giroday *et al*., 2012). Furthermore, the successful dispersal hinges on the organism's dispersal capacity and the suitability of habitats beyond its historical range, e.g. *T. pityocampa* in the Italian Alps (Battisti *et al*., 2006). Finally, given that newcomers successfully arrive at the novel location, they must occur in enough numbers to establish a reproducing population there (Allee effect; Tobin *et al*., 2011). Although these three processes are likely to be identical for most insect species, the nature of the establishment of a reproducing population is particularly interesting for the present discussion; the environmental factors prevailing in the novel locations will determine whether or not the pest in the historical range will also reach pest status in the new location. Obviously, all the species in Category 1 are examples of this. For species in the other two categories, this is much more difficult to know. In particular, because predictions from envelope models are based entirely on climatic correlations in present ranges, it is virtually impossible to know whether or not populations in the new range will reach pest status (for example, due to biotic resistance in the new habitat). It should be noted also that new host plants can be encountered during the expansion, and sometimes result in host shifts (Clark *et al*., 2014), and this may affect both the insect pest and its natural enemies, with population consequences difficult to foresee (e.g. Raffa *et al*., 2013).

To conclude, as has been suggested repeatedly in the literature, because of their ectothermic lifestyle, it is reasonable to assume that a changed climate will have consequences for insect pest distribution and abundance. A critical read of the scientific literature, however, results in surprisingly few documented examples of climate change-induced range expansion. It should be remembered that long-term trends in the distribution and abundance of insect pests is notoriously difficult to document. Thus, it is possible that many more insect pests could have responded to climate change, or are likely to do so in the near future, than can be detected in the databases presently available. It is also possible, however, that biological systems, including insect pests, are less sensitive to direct climate effect than previously thought (due to the buffering effects of trophic interactions). We believe that both explanations apply. It is also likely that pest responses to climate change are individualistic (Lawton, 2000). Thus, future research needs to focus more on developing process-based understanding of responses to changed climate (Schurr *et al*., 2012) in order to understand better, and predict more accurately, the likelihood that insect pests will expand their outbreak range.

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2 Species Distribution Modelling in Predicting Response to Climate Change

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Abstract

Species distribution modelling comprises a range of widely used tools for predicting potential changes in insect pest species distributions with climate change. We review the current literature to see the effectiveness of different approaches, particularly in comparing predictions based on current distribution data (correlative or ‘environmental niche models’) and those based on life-history traits and determination of thermal limits (mechanistic models). We review new developments in implementing processes such as dispersal and biotic interactions within species distribution models and how these could be used to develop management strategies incorporating natural enemies into climate change predictions. We propose that species distribution models should be linked with key trait data where possible to inform better of response to climate change.

2.1 Introduction

Many species of invertebrates not only cause huge losses to biodiversity through competition and disruption to ecosystem function (Ostberg *et al*., 2013; Zhou *et al*., 2013), but also represent some of the most recognized causes of agricultural crop loss through both herbivory and competition, and as vectors of disease (Ziska *et al*., 2010). Further to this, there are many invertebrate species that pose serious concerns for human health, particularly mosquito vectors (Bai *et al*., 2013; Lee *et al*., 2013) and ticks (Morin and Comrie, 2013; Porretta *et al*., 2013). Climate change will result in a range of potential impacts on pest invertebrates (reviewed in Harrington and Woiwood, 1995), including changes in population dynamics such as growth rate and overwintering success, as well as an increase in the number of generations per year and changing interactions with other species (Van der Putten *et al*., 2010; Sutherst *et al*., 2011). Greater risks are likely to come from changes in geographic distributions of pests and invasions by new pests (Harrington and Woiwood, 1995). For example, the distribution shifts and greater outbreak potential of the coffee borer beetle, *Hypothenemus hampei* Ferrari, in Africa (Jaramillo *et al*., 2009), and the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in North America (both Coleoptera: Curculionidae) (see de la Giroday *et al*., 2012), and the pine processionary moth, *Thaumetopoea pityocampa* Schiff (Lepidoptera:

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Thaumetopoeidae), in Europe (Battisti *et al*., 2005), are all linked to climate change.

Pest invertebrate species cause extensive damage to a wide range of economically important industries such as fruit and horticulture, pasture and broadacre crops including oilseeds, cereals and pulses. While drivers such as changes in pesticide use and increased irrigation are likely to be associated with some shifts in species distributions, climate change is likely to be driving shifts in the geographic distribution of some pest invertebrate species (Hoffmann *et al*., 2008). With changes in distribution come changes to phenology and persistence that ultimately lead to pest outbreaks and spread of vector-borne plant pathogens. Some species, such as armyworm (Lepidoptera: Noctuidae), may be responding negatively to climate change (Hoffmann *et al*., 2008). Others, such as the slug, *Milax gagates*, which perform better in arid conditions, may benefit from drier conditions under climate change (Nash, 2008; Domisch *et al*., 2011; Jiang *et al*., 2013), and so too the transmission of plant viruses, such as Yellow dwarf by aphid vectors (Parry *et al*., 2012). Clearly, pest species will respond to climate change differently, and it is thus important to investigate individual species' responses through a framework that is broadly applicable.

To meet the challenges that climate change will impose on food production, we need to be able to predict accurately how pest species will respond. To date, research on how invertebrate pests will respond to climate change is relatively rare (Mika *et al*., 2008; Ziter *et al*., 2012). Such research could help in the development of management recommendations to be used by growers to aid crop protection in the future (Steffen *et al*., 2011; Turner *et al*., 2011). For this to be achieved, a good understanding is required of how species have adapted in the past, how they respond to current variability in weather, and when and how this is likely to lead to pest outbreaks across agricultural landscapes. An essential component of this is to predict species distributions across the landscape.

2.1.1 Predicting distributions of pest insects

The link between insects and climate was researched widely even before the field of ecology was formally recognized. When Uvarov (1931) reviewed this subject, he cited over 1000 papers, many of which dated back to the 19th century or earlier. At this time, the field of 'climatic analysis of insect distribution' was first formulated. Meteorological data were available to ecologists and the understanding of how large-scale climatic variables influenced distributions was becoming apparent (e.g. Grinnell, 1917). While there existed a few studies that studied the effect of climatic variables on pest insects: for example, alfalfa weevil (Ball, 1917), green bug, *Schizaphis graminum* Rond. (Ruggles and Wadley, 1927), and Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Gjullin, 1931), it was William C. Cook who outlined methods of predicting the distributions of pest invertebrate species (Cook, 1931). Within these methods, Cook (1929) described how weather station data could be used initially to determine climatic zonations for pest insects. He explained how these zones could be correlated with the frequency of limiting climatic conditions and thus provide maps describing where outbreaks of species such as the pale western cutworm, *Porosagrotis orthogonia* Morr. (Cook, 1924), and the true armyworm, *Cirphis unipuncta* (now *Mythimna unipuncta* (Haworth)) (Cook, 1929), were more likely to occur. Cook went on to describe a framework for predicting insect distributions that tied weather data to insect distributions and known physiological parameters (Cook, 1931). While the effects of 20th century climate change were not apparent at this time, and the field of invasion biology was just emerging, this provided a robust framework for predicting the distributions of pest invertebrates in relation to climate. (For another account of Cook's contribution to the field of predicting pest insect distributions in relation to climate, a recent paper by Sutherst (2014) gives further detail.)

There have been many other advances in the field of pest ecology and distributions since the time of Cook (e.g. Messenger, 1959; Andrewartha and Birch, 1982), but predicting the distribution of a pest species still remains an essential component of understanding the potential effects of climate change. Today, we are faced with enormous challenges posed by a changing climate and increasing introductions of insect pests through global trade and tourism, and we require tools, methods and competent practitioners to meet them.

In this chapter, where we review the prediction of pest invertebrate response to climate change through the use of modern tools, it is still useful to consider the ideas of Cook (1931). Central to predicting potential distributions for pest insect species and response to climate change is the concept of the *niche*.

2.2 Niche Concept

2.2.1 Niche definitions

The niche is an ecological concept that ties biotic and environmental elements together (Keller and Golley, 2000) to define the distribution or functional role of a species. To describe the niche for a given species accurately would involve measuring every environmental condition, biotic interaction and resource that an organism requires (Porter and Kearney, 2009). In reality, this is an impossible task; however, the niche as a concept still serves as a useful tool for understanding species' requirements across space and time (Soberón and Nakamura, 2009; Wiens *et al*., 2009). In terms of predicting the distribution of species, there are different and equally important interpretations of the niche that need to be defined when investigating processes and traits that determine niche boundaries (Colwell and Rangel, 2009; Porter and Kearney, 2009; Wiens *et al*., 2009).

The first formal definition of the niche was provided by Joseph Grinnell, who described the niche in terms of areas of distributions of species and the different variables that govern the range of species (Grinnell, 1914, 1917). That is to say, that the spatial extent of the range and geographical expression of a species' niche are approximately the same (Tingley *et al*., 2009). This provides a somewhat restricted definition of the niche, employing broad, non-interacting ecological variables (Soberón and Nakamura, 2009) to set the range limits of species (Wiens, 2011). This simplicity allows for an operational and straightforward niche concept (Soberón and Nakamura, 2009) and, when employed, can provide strong explanations of species' range boundaries (Tingley *et al*., 2009). Such an interpretation of the niche lends itself to being particularly useful in understanding biogeographical patterns (Wiens, 2011).

While the Grinnellian niche encapsulates broad environmental processes, Charles Elton defined the niche in terms of biotic interactions and resource limitations that shaped the distribution of a species (Elton, 1927; expanded by Soberón, 2007). This interpretation of the niche presents the species as playing a functional role within a community (Wiens *et al*., 2009), and is thus a much finer-scale concept than that of Grinnell. The Eltonian niche employed axes of resource utilization and provided the foundation for later elaborations by Hutchinson (1957) and MacArthur (1972), to become widely used in ecological studies (Wiens *et al*., 2009). This interpretation of the niche allows for understanding of the biophysical requirements of the species to be measured and associated with landscape features, to define niche boundaries.

In later development of the niche concept, George Evelyn Hutchinson (1957) presented a niche–distribution duality that provided perhaps the most important distinction of niche concepts termed fundamental and realized niches. Hutchinson described the niche as taking both the form of the *fundamental* niche – the direct physiological requirements of a species – and the *realized* niche – the proportion of the fundamental niche actually occupied by the species at a particular time, due to limits set by both biotic and abiotic interactions (Wiens *et al*., 2009). This Hutchinsonian definition of the niche allows for both the Grinnellian and Eltonian niche interpretations to be employed in a suite of species–environment relationships within physical (environmental) and geographical (biotope) space (Colwell and Rangel, 2009; Wiens *et al*., 2009).

The growth of species distribution model use has seen the advent of the *potential* niche. This describes the area that might permit population persistence and growth, but to which the species has not yet dispersed (Soberón, 2007; Soberón and Nakamura, 2009). This concept is particularly important for pest and other invasive species that are not in equilibrium with the environment.

2.2.2 Niche conservatism

When measuring the response of pest insects to climate change, it is important to understand how the species–environment relationships are likely to persist or change. A species that occupies geographical regions corresponding to regions of niche space set by the fundamental niche is said to have displayed niche conservatism (Colwell and Rangel, 2009). Conversely, niche 'shifts' describe transgression between species–environment relationships across ranges (e.g. Broennimann *et al*., 2007; Fitzpatrick *et al*., 2007) or over time (e.g. Kharouba *et al*., 2009). For studies of climate change, niche conservatism refers to species that track climatic change to preserve species–environment relationships: species must undergo elevational and/or latitudinal range shifts to stay within their favourable climate zones (Colwell and Rangel, 2009). This process can cause problems for species not able to disperse as fast or as far as the changing climate dictates.

Niche shifts may occur if the native range holds only a subset of the full range of the fundamental niche due to interspecific competition (the presence of predators and pathogens), or a geographical barrier, or a limited set of possible environments – the species in its invasive range might simply be expressing other parts of the fundamental niche (Broennimann *et al*., 2007; Rödder and Lötters, 2009; Alexander and Edwards, 2010; Medley, 2010). Alternatively, the species may have adapted, resulting in a change in a species' response to environmental variables over time (Broennimann *et al*., 2007; Ficetola *et al*., 2010). A niche shift may also arise through species dispersal and colonization, driving expansion geographically into new environmental habitats (Alexander and Edwards, 2010). These processes of range expansion may be facilitated by changes in climatic conditions, land use or through evolutionary adaptation.

Measuring niche conservatism can give insight into predicted pest insect response to processes such as climate change and biological invasion, including the interaction of these two. In this chapter about modelling insect pests and climate change, we describe tools to measure niche conservatism geographically and look at examples from both biological invasions and climate change research, as these fields are highly relevant to one another. One way in which we can study the process of niche shifts and niche conservatism in response to climate change is to construct different types of species distribution models. These models can be used to inform which environmental variables and traits may limit the niche, and the level of niche conservatism displayed in species invasion and response to climate change.

2.3 Species Distribution Models

Species distribution models are increasingly popular tools for describing the niche of a species and detecting niche shifts. There are a number of modelling methods available that have varying advantages and explicabilities, and which utilize different interpretations of the species niche. Commonly used in conservation biology research (Pearson *et al*., 2007; Habel *et al*., 2011), species distribution models may also be applied to invertebrate pest species, especially when questions need to be asked of species invasion or climate change impacts. Importantly, the choice of which type of model to use relies heavily on the type of data you have available. It is also crucial that as much information about the species as possible is included to ground some of the choices during the modelling process.

Table 2.1 gives examples of recent research showing the application of species distribution models for a variety of pest insects. At present, the majority of pest insect distribution models determine potential areas for species invasions, though more are starting to address responses to climate change.

Much of the recent advance in species distribution modelling has been made possible by the increasing availability of global weather station data and the computational power to process these. This has allowed for the formation of geospatial databases that offer high-resolution layers of averaged monthly climate data (e.g. WorldClim (Hijmans *et al*., 2005), ANUCLIM (v6.1, Fenner School of Environment and Society, Australian National University)). These data can be transformed into biologically relevant trends and patterns of rainfall, temperature, humidity and solar radiation (e.g. BIOCLIM variables (Nix and Busby, 1986)), and used to determine limiting factors to species distributions (Elith and Leathwick, 2009). Instead of models being restricted to a few sites, it is possible to project models across entire countries, continents or globally, to understand the macroecological processes of invasion and climate change (Peterson, 2003; Araújo *et al*., 2005; Elith and Leathwick, 2009). There is also a range of future climate models (global circulation models – GCMs) that are based on different scenarios of the severity of climate change. These allow for future forecasts of climate change to be incorporated into species distribution models. Choice of climate change scenario can alter model outputs, so this needs to be taken into consideration when building models, to determine which scenarios are likely to be relevant to the models (Beaumont *et al*., 2008; Mika and Newman, 2010). As no one model may be considered the ‘best’ (Beaumont *et al*., 2008), an ensemble forecast of a range of GCMs can outperform single GCMs and provide greater confidence in model outputs (Fordham *et al*., 2011).

While the toolbox is increasing for species distribution modelling, there is little chance that automation will ever take hold (see Sutherst, 2014), and generalizations are likely to be only for large-scale studies rather than for effective management at the landscape level (e.g. general poleward movements; Bebber *et al*., 2013). Selection of the most appropriate model requires careful consideration of the species and the data available for the species, which will be different in terms of forms and amount. There is no ‘one size fits all’ approach for modelling pest insect species, and this needs to be taken into consideration. The range of models presently available are suited to different tasks and use types of data in different ways, and it may often be that applying different types of models to the same species, allowing for determining congruence between predictions, is a better approach (Venette *et al*., 2010).

There is a wealth of literature on the application of different species distribution models, and there are many debates surrounding the application and validation of such models. Here, we present a brief overview of the currently popular methods of species distribution models being applied to questions surrounding pest insects and climate change; ecological niche models, mechanistic models and a semi-mechanistic approach, CLIMEX (see Fig. 2.1).

2.3.1 Ecological niche models

Species distribution models that attempt to characterize the niche by correlating known distribution points with environmental predictor variables, or covariates, are typically referred to as ecological niche models (ENMs) (Jiménez-Valverde *et al*., 2011; Wiens, 2011). ENMS investigate something close to the realized or potential niche of a species by correlating limiting variables identified from the landscape the species is found in to suitable habitat in appropriate geographic areas (see Elith

Table 2.1. Examples of species distribution models for pest invertebrate species.

Common name	Species	Models	Type	Use	Locality	Reference
Fig fly	*Zaprionus indianus*	MAXENT/GARP/ Mahalanobis distances	Correlative	I	Global	da Mata *et al*., 2010
Western corn rootworm	*Diabrotica virgifera virgifera*	ENFA/Mahalanobis distances	Correlative	I/C	Northern hemisphere	Aragón and Lobo, 2012
Yellow-legged hornet	*Vespa velutina nigrithorax*	Ensemble modelling	Correlative	I/C	Global/Europe	Barbet-Massin *et al*., 2013
Mediterranean fruit fly/ Natal fruit fly	*Ceratitis capitata/Ceratitis rosa*	GARP/PCA	Correlative	I	Africa/Europe/global	De Meyer *et al*., 2008
Asian tiger mosquito	*Aedes albopictus*	CLIMEX/MAXENT	Semi-mechanistic/ correlative	I/C	Australia/global	Hill *et al*., 2014
European grapevine moth	*Lobesia botrana*	Physiology/demographic	Mechanistic	I	California/USA	Gutierrez *et al*., 2012
Light brown apple moth	*Epiphyas postvittana*	Temperature/demographic	Mechanistic	I	California	Gutierrez *et al*., 2010
Light brown apple moth	*Epiphyas postvittana*	CLIMEX/MAXENT	Semi-mechanistic/ correlative	I	Global	Lozier and Mills, 2011
Bird cherry-oat aphid	*Rhopalosiphum padi*	CLIMEX	Semi-mechanistic	I	Global	Macfadyen and Kriticos, 2012
Pea leafminer	*Liriomyza huidobrensis*	CLIMEX	Semi-mechanistic	I/C	North America	Mika and Newman, 2010
Swede midge	*Contarinia nasturtii*	CLIMEX	Semi-mechanistic	I/C	North America	Mika *et al*., 2008
Spruce budworm	*Choristoneura fumiferana*	Ecophysiology/temperature	Mechanistic	C	North America	Régnière *et al*., 2012
Brown marmorated stink bug	*Halyomorpha halys*	MAXENT	Correlative	I	North America/global	Zhu *et al*., 2012

Note: I = invasion risks; C = response to climate change.

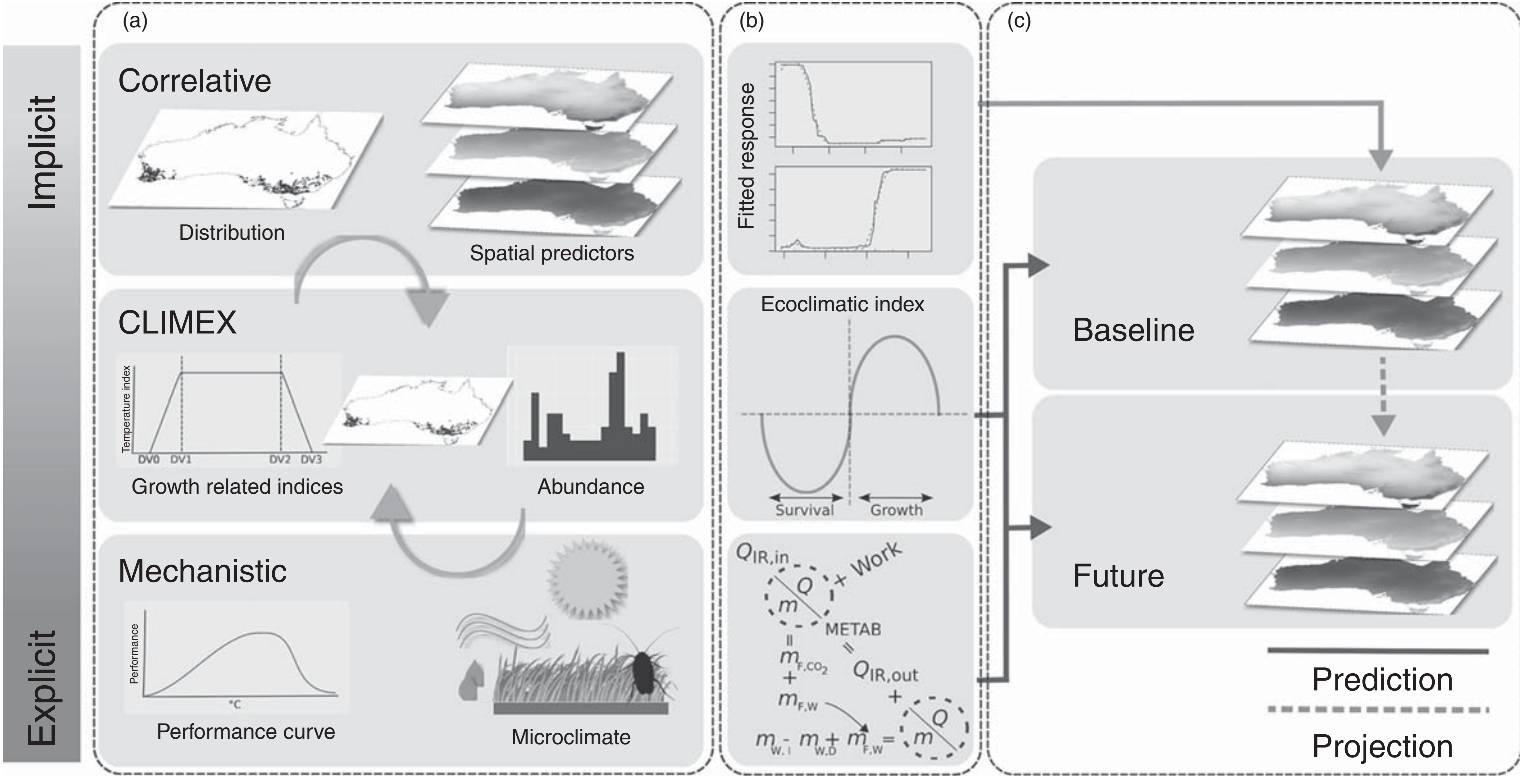

Fig. 2.1. Schematic illustration showing general differences between types of species distribution models (SDMs) used in predicting the response of insect species to climate change. (a) Displays the different categories of SDM mentioned in this chapter and the data sets they incorporate. (b) Displays how those data are fitted in the model. (c) Displays how the fitted models are then either spatially predicted or projected to new climate surfaces. Explicit and implicit scale is adapted from the review in Kearney and Porter (2009). *Correlative models* (typically called *ecological niche models*) combine known localities of species (presence-only or presence-absence records) with spatial predictors at each of these locality points to model species–environment relationships. Fitted functions for response to incorporated variables are then combined to determine the species–environment relationships, and then this can be predicted to the spatial data the model was trained on, or projected (extrapolated) on to new spatial predictors, such as climate change scenarios.

continued

et al., 2011 for a more detailed explanation). Using such models, it is possible to predict pest insect species range boundaries and project these models into future climate change scenarios (extrapolation) to investigate how changing climate space may influence broad-scale species–environment relationships.

There is an increasing variety of correlative methods available to predict the distribution of species, ranging from regression methods such as GLMs (generalized linear models) and GAMs (general additive models), bioclimatic methods such as BIOCLIM and ENFA (environmental niche factor analysis) and through to more recently developed machine-learning methods, MAXENT (maximum entropy) and BRTs (boosted regression trees). A prerequisite for using all these types of ENMs is having sufficient distribution data to characterize the species–environment relationships across the geographical ranges that are likely to determine the distribution. In turn, good distribution data provide a clear advantage of a robust model being built, with little knowledge of the species' ecology and biology required (although to present a model in isolation of this will provide little benefit). One of the key points of using distribution information is that these points are the result of many different ecological processes (Sutherst, 2014). That is, when applying correlative models, the data being included could represent any number of possibilities that translate into a presence point. Presence points do not always represent population persistence, and thus it is imperative to understand which data are useful to the modelling process.

Different forms of distribution data will again dictate which of these model types is most appropriate to the species question in hand, including amount of distribution points, the prevalence of those points across a given area and whether there is absence data as well as presence data. For instance, MAXENT and ENFA require presence-only data (with an ecologically defined background, or study area), whereas BRTs can employ presence and true (surveyed) absence data. What ENMs all have in common, however, is the requirement of well-sampled and unbiased data to construct models that encapsulate as broad a range of species–environment relationships as possible. Ideally, species–environment relationships in both the native and invasive ranges need to be characterized (Beaumont *et al*., 2009; Jiménez-Valverde *et al*., 2011). For many pest insect species, the only data available are for where a species has been found (e.g. outbreaks) or abundance data, thus the correlative models in Table 2.1 are all based on presence-only data. These data need to be checked closely for errors, and often require expert opinion to confirm the validity of distribution data. For more information on spatial biases and sampling errors and how they influence models, Dormann *et al*.

Fig. 2.1. *continued*

CLIMEX draws from different knowledge domains (e.g. physiological response, distribution data and abundance data) to determine an ecoclimatic index that is a combination of growth and stress indices (redrawn from Sutherst *et al*., 2004). This is run across weekly values throughout a year and then combined into a yearly summary of population growth and survival seasons (adapted and redrawn from Sutherst, 2003). In this way, models can be run for a given locality or across gridded spatial predictors, to produce maps of geographic suitability based on the ecoclimatic index. By running the model on future climate scenarios, CLIMEX is able to avoid the inherent issues of extrapolation that correlative models incur.

Mechanistic models take physiological information measured on the species to define limits to distributions based on processes and ecophysiological profiles. While mechanistic or process-based models can take many forms, the stylised one here combines performance curves and information about the microclimate (adapted, with parts redrawn from Kearney and Porter, 2009). Models can be based on how the species experiences the environment, how this affects metabolic rate and what this ultimately means to distributions and phenology under both current (baseline) and future conditions. Additionally, mechanistic models may be able to incorporate biotic interactions as explicit processes to examine the effects of climate change on pest insects and competitors/predators (see text for more detail).

(2007) and Elith and Leathwick (2009) provide reviews.

Because biotic and abiotic factors, and dispersal constrain the niche, ENMs can provide only partial information on the full range of environmental conditions that the species may survive (i.e. not estimating the fundamental niche, or even the potential niche) (Jiménez-Valverde *et al*., 2011). Related to this there are two main criticisms when using correlative models for measuring biological invasion and response to climate change.

The first of these criticisms is that environmental limits may be different between populations (particularly across both native and invasive ranges), inhibiting the ability of models to describe both ranges (Randin *et al*., 2006). For instance, when characterizing the realized niche of the native range, the species may be inhibited by a range of barriers, including biotic and abiotic factors that do not exist in the invasive range (Beaumont *et al*., 2009), resulting in underestimation of the potential invasive niche. Further, insect pest species are often not in a state of equilibrium with their environment, particularly within novel, invaded ranges (Václavík and Meentemeyer, 2009). This may translate into geographic range expansions as species continue to spread to fill their potential niche (Soberón, 2007; Soberón and Nakamura, 2009) and give rise to issues with ENM predictions. However, there are some techniques to help with these issues; see Elith *et al*. (2010) and Hill and Terblanche (2014) for examples of using presence-only data for range-expanding species. This non-equilibrium may be further exacerbated through climate change.

The second group of criticisms surrounds the use of ENMs as reliable tools for extrapolating into new space or time. Some degree of caution must be taken when projecting ENMs, as the relationship of variables projected may result in underprediction of areas that will contain non-analogue climates. Therefore, when ENMs are used to measure niche conservatism and response to climate change, they inherently encompass a broad range of factors and include the possibility that niche shifts are not a result of change in the fundamental niche (Hill *et al*., 2012). A good primer on the application of the transferability of correlative species distribution models is found in Elith and Leathwick (2009).

In the absence of strong biotic interactions, as is often the case for pest insect species, it is possible to explore modelled responses and apply ENMs in an attempt to account for unstable relationships with climate, and as yet unencountered environmental conditions (e.g. Elith *et al*., 2010) such as climate change. Given good distribution data in both native and invasive ranges (characterizing the realized niche as much as possible), correlative models have been demonstrated to be valuable tools for modelling pest insect distributions in relation to climate change.

2.3.2 Mechanistic models

Mechanistic models are often referred to as process-based (Morin and Thuiller, 2009) or trait-based (Kearney *et al*., 2008) models and use explicit biological processes built on species-specific observations (Morin and Thuiller, 2009). In this regard, mechanistic models are often able to overcome some of the main issues associated with using ENMs, such as when they are employed to investigate species response to climate change, they are not extrapolating from inferred relationships measured through distribution data but rather aim to translate morphological and physiological traits of a species with key environmental variables and the terrain (Kearney *et al*., 2008; Kearney and Porter, 2009). This means that mechanistic models require little to no information about the distribution of a species to construct the model (Kearney *et al*., 2008), which may be much more suited to a pest insect species of which little is known about the origin or geographic distribution but there is the ability to characterize life tables and trait data.

While mechanistic models are not always used for species distributions, they can be projected on to spatial data (e.g. GIS data), like those used as predictor variables in correlative models, to determine the probability of a given location, or grid cell, to meet the organism's resource requirements (Kearney and Porter, 2004). Information regarding physiological response to climatic variables can be compiled into a framework to understand activity, reproduction and survival thresholds. Mechanistic models that may be most useful for the prediction of pest invertebrate distributions include life history and phenology models (e.g. Gutierrez *et al*., 2008, 2010, 2012) or thermodynamic niche models (e.g. Kearney *et al*., 2008; Kearney and Porter, 2009). Like correlative ENMs, they can be interpreted through the Hutchinsonian niche duality, but instead characterize axes of the fundamental Eltonian niche. Mechanistic models can also include information about the microclimate – the environmental conditions an individual of a species will experience and utilize (Kearney *et al*., 2009).

The downside of using mechanistic models in pest insect species distribution modelling is that this avenue is often data intensive, and thus a single species requires much research attention. This may be possible for established pest species that often have a long history of research interest, resulting in data accumulation (e.g. light brown apple moth, *Epiphyas postvittana* Walker, pine processionary moth, gypsy moth, *Lymantria dispar* L., mosquitoes including *Anopheles* and *Aedes* spp., and others), but not so much for emerging pests that require immediate attention. When sufficient data are available though, mechanistic models are very appropriate and allow for more in-depth analyses of species response to climate change. This is particularly evident for species that are in a state of flux or range expansions (filling potential niche), or through adaptive changes in physiological or morphological traits. Species that are in the process of such adaptive shifts (e.g. the cane toad, *Bufo marinus*) may prove challenging to apply ENMs (Kearney *et al*., 2008), unless different weightings and model complexity parameters are explored, grounded on other biological information (Elith *et al*., 2010). This is important in terms of understanding the effects of climate change on pest invertebrates, as research should aim to include both phenotypic and genotypic flexibility (Bale *et al*., 2002). Mechanistic models can incorporate levels of variation or plasticity in distribution-limiting traits (Kearney and Porter, 2009; Kearney *et al*., 2009; Kolbe *et al*., 2010), which allows for hypotheses of adaptive shifts to be estimated under selective conditions such as climatic change.

Mechanistic models that incorporate trait variability (e.g. Kearney *et al*., 2009) provide an alternative to using an ENM-centred framework. However, while mechanistic models that characterize the thermodynamic niche (e.g. Kearney *et al*., 2013) provide comprehensive detail, these require many parameters and extensive empirical research. By having a mechanistic understanding of how climate affects life-history traits such as emergence (e.g. Kearney *et al*., 2010), and number of generations, it may be possible to translate these into guidelines for control measures. Finally, as they are based on explicit processes, mechanistic models are also able to take directly into account other environmental processes, such as biotic interactions. We talk more about this later.

2.3.3 CLIMEX

One of the most common modelling tools used for pest insect distributions is CLIMEX (Sutherst and Maywald, 1985). This tool uses a process-fitted or semi-mechanistic approach to examine the relationship between climate, species distributions and patterns of growth (Macfadyen and Kriticos, 2012). Importantly, CLIMEX models can be fitted using a combination of empirically measured parameters, abundance and point distribution records. These data types are often complementary for insect pest species and allow for knowledge gaps to be bridged when constructing informative models. Hence, CLIMEX is ideal for modelling distributions of pest insects, as it often is that data are 'patchy' across abundance, distribution information and physiological information (such as life-table studies).

The CLIMEX model works through a series of weekly growth and stress indices that are combined to produce an ecoclimatic index (EI). The EI describes regions that are unsuitable for the species to persist, through to those that provide a 'perfect' environment for the species. This is interpreted within a scale of 0–100 (Olfert *et al.*, 2011), with an EI over 20 considered to convey ideal conditions (Sutherst *et al.*, 2004) and below 10 an unfavourable environment, though rating interpretations will be species specific to some extent. The strength of CLIMEX lies in its ability to project models to new environments without relationships between variables confounding projections. CLIMEX also has a lot of flexibility; for example, when abundance patterns are not well known, they can be inferred from development rate experiments or observations and these become methods of validation (Kocmánková *et al.*, 2011; Macfadyen and Kriticos, 2012).

The coupling of demographic parameters with spatial distribution information and other different data types gives CLIMEX certain advantages over SDMs and allows for basic physiological information (e.g. response to temperature, moisture) to be incorporated into climate change projections. CLIMEX is able to avoid some of the issues involved with transferability associated with ENMs, due to the model being built on climate change data rather than being extrapolated. This makes CLIMEX suited to predicting new geographical regions for invasive invertebrate species, and also responses to climate change. However, the stress indices are normally derived from the realized distribution and, due to the nature of the climate data used, CLIMEX models do not capture microclimate effects. In this way, CLIMEX is closer to a correlative approach, an important consideration when employing this model type.

Another advantage to using CLIMEX is that it is also able to investigate evolutionary adaptation indirectly by adjusting parameters based on information about changes in physiological tolerances. For example, Hill *et al.* (2014) looked at the mosquito vector of Dengue fever, *Aedes albopictus*, and incorporated different physiological profiles (based on experimental data on adaptive change) to examine how the species might respond to climate change given a shift in temperature tolerance.

2.3.4 Other models

Besides the main types we have just presented, there is a range of other models available to model insect pests and their response to climate change. One that looks particularly applicable is the Insect Life Cycle Modeling (ILCYM) software (Sporleder *et al.*, 2009), which can be used to determine the number of generations in a given geographical area under different climatic conditions (Kroschel *et al.*, 2013). A phenology model like ILCYM could determine if suitable climate space determined by ENM methods would translate into faster population growth for different pest insect species. This coupling of methods would provide some valuable insight into pest insect species and climate change.

As climate change is likely to affect processes beyond what any one modelling process can capture, it may be important to combine multiple modelling methods (e.g. ENM, semi-mechanistic, phenological and thermodynamic mechanistic models). Using combinations of models to assess the response of pest insects to climate change may translate into more targeted management decisions. For example, using CLIMEX alongside ENMs allows for areas of congruence to be assessed (e.g. Lozier and Mills, 2011; Hill *et al.*, 2014).

2.4 Current Developments/Future Directions

So far in this chapter, we have considered species in isolation, and without considering dispersal ability. Both the interactions with other species and the ability of species to move both actively and passively are likely to play major roles in determining response to climate change. Here, we review current developments in each of these categories and suggest ways in which they may be incorporated in predictive modelling of pest insect species.

2.4.1 Biotic interactions

One of the main limitations when applying SDMs to a single species is that each species is considered in isolation and as a single population. Species, of course, do not exist free from interactions with other species, nor are they homogeneous in response to environmental stressors. Interactions such as competition, predation and parasitism are all likely to be impacted by climate change, resulting in species composition shifts and biocontrol failures (Sutherst *et al*., 2007; Thomson *et al*., 2010). Ecologists increasingly recognize the importance of species interactions for mediating the effects of climate change (reviewed in Tylianakis *et al*., 2008; Gilman *et al*., 2010; Walther, 2010; Yang and Rudolf, 2010).

Biotic interactions (e.g. competition and predation) may restrict the spread of pest invertebrate species (i.e. a new predator encountered in an invasive range, or competitive interactions between species) under present climatic conditions, but these interactions may mismatch through shift under climate change, resulting in altered pest invertebrate distributions. Biotic interactions also impact on population abundance across time, limiting species distributions spatially. In terms of biocontrol, beneficial (predators and parasitoids) species may respond to climate change in completely different ways than the pest invertebrate they attack (Thomson *et al*., 2010). Thus, the influence of biotic interactions and their success under a changing climate needs to be considered, and at what spatial scale these interactions are important. For instance, it may be argued that for some species models that incorporate broad climatic variables, biotic interactions may not be important in shaping the distribution at that scale, only at a finer, landscape level. Further, some pest insect species are highly successful competitors and biotic interactions are unlikely to limit distributions outside their native range (e.g. *Bactrocera invadens*; Hill and Terblanche, 2014).

Incorporating interactions in species distribution models has proved a challenging area of research. Species interactions are currently incorporated in ENMs at a basic level, including covariates of competitive interactions (Pellissier *et al*., 2010; Meineri *et al*., 2012) and available prey items (Hof *et al*., 2012), to look at how these interactions affect modelling outcomes. Another approach that looks promising is to nest a community of species spatially within a modelling framework that incorporates co-occurrence indices (Boulangeat *et al*., 2012). Population processes such as dynamic ranges and dispersal parameters can also be incorporated into ENMs. Developments in this area include dynamic range models (DRMs) to estimate spatial population dynamics (Pagel and Schurr, 2012; Schurr *et al*., 2012) and other dynamic species distribution models that can incorporate stochastic processes such as dispersal, growth and competition within a Bayesian framework (Marion *et al*., 2012). Processes such as biotic interactions and dispersal could also be linked explicitly within a mechanistic modelling framework, and there are simple interaction parameters available for CLIMEX models to examine changes in the EI under climate change (Sutherst *et al*., 2007).

In considering pest invertebrates and climate change, it is important to consider the types of biotic interactions that may play a role in shaping responses. These may include competition, natural enemies' interactions and host shifts. Some of the avenues for incorporating biotic interactions within SDM frameworks are presented in Kissling *et al*. (2012), highlighting an exciting area of SDM research that will enhance greatly climate change predictions for pest insect species.

Competition

The varying success with which a pest invertebrate species outcompetes endemic and/or other pest species has implications for predicting distributions accurately, both currently and under climate change. The potential importance of competition in determining distributions is demonstrated by the highly successful invasive ladybird beetle, *Harmonia axyridis* (Pallas), where its success in interspecific competition is implicated in adverse ecological impacts through North America and Europe (Roy *et al.*, 2012). Further, the thrips species, *Frankliniella occidentalis* (Pergande), is a highly invasive pest that has spread from its original range (the western states of the USA) to a worldwide distribution. Despite this, it is largely absent in the eastern states, where a native thrips, *Frankliniella tritici* (Fitch), successfully outcompetes in larval competition (Paini *et al.*, 2008). While there are currently limited examples for pest insects, there are some recent studies looking to incorporate competition into SDM, particularly ENM, approaches. For example, Brame and Stigall (2014) used ENM modelling to reconstruct ecological niches for 11 genera of marine invertebrates over geological time and found taxa adjusted to increased competition by altering aspects of their niche. These types of studies may serve as valuable road maps for incorporating competition into climate change predictions for insect pests.

Predators/parasitoids or natural enemies

The impact of predators and parasitoids on invertebrate pests is well documented, and the presence or absence of natural enemies has been demonstrated to exert a controlling influence on pest insect species distributions (Thomson *et al.*, 2010; Culik *et al.*, 2013). In the absence of parasitism, a mechanistic SDM predicted a wide geographic istribution of glassy-winged sharpshooter (*Homalodisca vitripennis* (Germar)) in the USA and Mexico. Including the interaction with its egg parasitoids (*Gonatocerus ashmeadi* Girault and *Gonatocerus triguttatus* Girault) in the model changed distribution predictions (and abundance) dramatically (Gutierrez *et al.*, 2011). In a well-studied species, more complex interactions may present themselves; for example, parasitoid attacks may induce different host immune responses, and some parasitoids may also make facultative response by adjusting life-history parameters. Larvae of the moth *Lobesia botrana* (Denis & Schiffermuller) can accelerate their development rapidly and reach maturity earlier in response to cues perceived at a distance from parasitoids. Such a phenotypically plastic life-history shift, induced by the perception of deadly enemies in the environment, is likely to be an adaptive defensive strategy to prevent parasitoid attack, and has important implications in host–parasite dynamics (Vogelweith *et al.*, 2013). A possible corollary of range shift moving from parasitoids extends to phenological change; loss of the cue allows longer development time of the moth. As hosts that mature earlier are smaller, which is often correlated with low fecundity and reduced longevity, maybe this is an advantage in a new environment, whether range change or invasion. Marini *et al.* (2013), in a long-term study aimed at identifying the role of predation and parasitism on bark beetles, concluded a limited effect. These kinds of complex interactions are largely unconsidered for pest insect SDMs, although they comprise key components in understanding the response to climate change and provide many opportunities for future research.

2.4.2 Dispersal ability

Further improvements to species distribution modelling may come from including dispersal information to examine how this influences response to climate change. Currently, most SDMs assume no dispersal, or unrestricted scenarios (see Travis *et al.*, 2013), while others attempt to combine dispersal information to SDMs through process-based modelling approaches (see Elith and Leathwick, 2009, for examples). For pest insect species, dispersal may be in either passive or active forms and play a major role in shaping the distribution. Dispersal may also introduce new species interactions, further highlighting the importance of movement of species as an important component to understand response to climate change properly. Newer methods such as DRMs, as presented in Schurr *et al.*

(2012), are able to incorporate dynamic processes such as dispersal and look promising for pest insect SDMs. Similar to this, population processes are likely to be useful for pest insect distribution modelling (Fordham *et al.*, 2013).

Current implementation of dispersal in pest insect distribution models includes the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), an invasive threat to North America (Fitzpatrick *et al.*, 2012). In this study, dynamic dispersal was combined with population processes and maps, characterizing heterogeneity in climate and habitat. Fitzpatrick *et al.* (2012) found that simulations generally matched the observed current extent of the invasion of HWA, but were not able to predict accurately when HWA was observed to arrive at different geographic regions. Differences between the modelled and observed dynamics were attributed to an inability to capture the timing and direction of long-distance dispersal events, which substantially affected the ensuing pattern of spread. Other weather events such as increased cyclones or high winds may increase dispersal beyond current conditions for some pests. Such events are inherently difficult to capture using current SDM techniques and corresponding meteorological information.

2.4.3 Genetic diversity

Another avenue to improve pest invertebrate SDM predictions is to incorporate relevant genetic diversity into the models. For example, ENMs typically assume that species exist as one large population, and therefore do not include potentially important difference responses between populations. If species distribution models are applied where clear structure exists between populations (for example, geographic barriers or multiple and distinct introductions), then it could be beneficial to examine the differences in environments occupied by populations or lineages (e.g. Arteaga *et al.*, 2011; Newman and Rissler, 2011). This can be achieved by identifying unique populations through measures of genetic divergence and partitioning model data into corresponding subsets, or perhaps information on dispersal and movement abilities of a species. While it is possible to measure population structure and divergence using microsatellites, for example, neutral genetic diversity and adaptive genetic diversity are often not correlated (Holderegger *et al.*, 2006). This implies that adaptive niche shifts that may alter response to climate change are not likely to be detected in such population genetic studies; instead, these studies provide information to calibrate modelling procedures around genetic diversity.

2.5 Enhancing Model Predictions with Niche-limiting Traits

As was pointed out when discussing the advantages of CLIMEX, data for pest insect species are often incomplete across the different knowledge domains (e.g. distribution information, physiological studies, demographic studies). A useful approach to predicting the effect of climate change on pest insect species may be to measure niche-limiting traits and then couple this with distribution information to detect variance and/or shifts and how they may influence potential response. We feel this is a framework that will prove to be more successful and draws from different knowledge realms in an insightful way. When applied appropriately, the different types of species distribution models are able to generate hypotheses about the niche of an organism, and then direct further research towards understanding traits that limit the niche (Rey *et al.*, 2012; Hill *et al.*, 2013). Adaptation in limiting traits may lead to niche shifts and mediate a species response to climate change (Chown *et al.*, 2010; Hoffmann and Sgrò, 2011). For the mosquito, *Aedes aegyptii*, Kearney *et al.* (2009) identified egg desiccation resistance as limiting the inland distribution of the species and incorporated this into a model predicting how adaptation in this trait could facilitate range expansion under climate change. Thus, one of the great challenges is to determine which traits may be limiting current distributions (Wiens, 2011) and then to measure these to incorporate them into predictions. Further, adaptation or persistence in changing environments may also be mediated through phenotypic plasticity: rapid phenotypic adjustment to environmental variation (see Chown and Terblanche, 2006). For invasive species, studies that measure traits in both native and invasive ranges, and across a range of environmental gradients, would be extremely beneficial, though are rare (Alexander and Edwards, 2010). The key traits that are relevant to niche shifts during invasion and under climate change are likely to be:

1. Thermal tolerance: maximum and minimum temperature limits for activity and survival. As temperature plays a large part in determining the niche of a species (Bale *et al*., 2002), understanding thermal tolerance traits can help to determine species–environment relationships (Terblanche *et al*., 2006). Thermal tolerance traits are used widely to investigate ecological and evolutionary processes for terrestrial arthropods (Hoffmann *et al*., 2005; Terblanche *et al*., 2006; Mitchell and Hoffmann, 2010; Alford *et al*., 2012). Species often exhibit differences in thermal tolerance limits across environmental gradients, including elevation and latitude (Gaston and Chown, 1999; Hoffmann *et al*., 2005), with variation across latitude, including phenotypic plasticity, more evident for lower than upper limits of terrestrial arthropods (Hoffmann *et al*., 2005; Terblanche *et al*., 2006; Alford *et al*., 2012; Hoffmann *et al*., 2013).

2. Desiccation resistance: water loss potential. For terrestrial arthropods, their small size and high surface-to-volume ratio means they are susceptible to desiccation (Johnson *et al*., 2011). Variation in desiccation resistance has been linked to distributional patterns (Kellermann *et al*., 2009). For example, tropical species of *Drosophila* have low desiccation resistance (and low heritability of this resistance), compared to widely distributed *Drosophila* species (Kellermann *et al*., 2009; Hoffmann and Sgrò, 2011).

3. Photoperiodism: physiological reaction to day or night length. While day length will not be affected by climate change, photoperiodism interacts with temperature and varies across latitude, to initiate lipid storage and diapause with the onset of winter (van Asch and Visser, 2007; Lehmann *et al*., 2012; Urbanski *et al*., 2012). Adaptation in photoperiodic response has allowed the mosquito, *A. albopictus*, to undergo range expansion in North America (Urbanski *et al*., 2012). Adaptations in photoperiodic traits may also facilitate earlier emergence (to coincide with milder winter temperatures) and increase herbivore damage under climate change (van Asch and Visser, 2007).

Photoperiodism can underlie different development patterns in a pest, which may facilitate population growth with changed temperature beyond what can be predicted with temperature modelling. Development times greater than explained by temperature differences in *L. botrana* in north-east Italy are interpreted as a means to ensure best fit of the moth to environmental conditions (Pavan *et al*., 2013).

Whereas mechanistic models can directly incorporate variation in niche-limiting traits, correlative models can determine which environmental covariates may be most important to the niche and which may limit the distribution of species across a geographic range. These can lead to hypotheses about which traits are likely to govern the distribution of the species and should be investigated empirically (e.g. Banta *et al*., 2012; Hill *et al*., 2013). This provides an opportunity to use correlative models in tandem with experiments to measure these traits, rather than building full mechanistic models, which can be time-consuming. Alternatively, a few niche-limiting traits for pest invertebrate species could be used with distribution information in CLIMEX-like models that are able to draw from multiple knowledge domains (Macfadyen and Kriticos, 2012).

For some pest insect species, it may be useful to characterize traits for other life stages, such as diapause, and look at intergenerational effects. This could form a comparison to ENMs and be projected on to the same future climate surfaces (e.g. the CliMond data set) to examine areas of model congruence.

2.6 Conclusion

Different pest insect species will respond to climate change in different ways. Species distribution models can provide important first steps in establishing hypotheses around the niche of a species, to drive hypotheses and experimental work for providing robust advice to managers and agricultural workers in the management of pests and global climate change. The type of distribution model to be employed should be based on data availability – combining from different knowledge domains where possible. When there is comprehensive and unbiased locality sampling, the increasing availability of interpolated weather station data facilitates approximation of the species realized niche using ENMs. Experimentally derived evidence allows for mechanistic models to predict response to climate change through an estimation of fundamental niche axes. The extensive data required are not always available, so tools such as CLIMEX allow for combination across data types. Generally, combining physiological, abundance and distribution data is likely to give better predictive ability.

Through measuring traits such as thermal tolerance, desiccation resistance and photoperiodism and combining this with model (e.g. ENM) predictions, valuable insights into species niche dimensions, and the added potential to investigate adaptive shifts, informs on species response to climate change.

Consideration of other drivers that shape species distributions, including biotic interaction such as competition, the presence of natural enemies and impacts of host shifts, have the potential to increase the accuracy of prediction. Predicting response to climate change for pest insect species will benefit greatly from advances in species distribution modelling to include knowledge of species dispersal ability and interactions, though all SDM work must serve as a guide to inform rather than determine management decisions under climate change.

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3

Adaptive Responses of Plants to Insect Herbivores under Climate Change

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Abstract

Global climate change, including the rise of CO_2 emissions and global warming, are predicted to alter the composition of communities through differential colonization abilities between sessile plants and their mobile insect herbivores along latitudinal and elevation gradients. In particular, under the scenario of increasing temperature, it is expected that insect abundance and diversity will increase at higher elevation and latitude. The outcome of novel interactions between previously non-overlapping plant and insect species will ultimately result from the ability of the plant to adjust its defence and tolerance strategy. However, plant responses to herbivory may also be directly impacted by the effect of CO_2 and temperature on plant defensive hormonal pathways. Additionally, syndromes of plant defences and tolerance are driven by inherited functional traits, biotic and abiotic conditions and the geographical and historical contingencies affecting the community. Therefore, understanding evolutionary species responses to climate change and novel plant–herbivore interactions requires understanding of genetic variation, strength of phenotypic plasticity in response to herbivore attack and trait phylogenetic conservatism. We advocate the study along elevation gradients for predicting ecological and evolutionary outcomes of climate change on plant–herbivore interaction.

3.1 Introduction

Longitudinal studies and long-term monitoring data are uncontestably showing that global climate change is having pervasive effects on plant and animal distributions and phenology (Grabherr *et al.*, 1994; Parmesan, 1996; Hoegh-Guldberg *et al.*, 2008; Stange and Ayres, 2010; Burrows *et al.*, 2011; Pateman *et al.*, 2012; Pauli *et al.*, 2012). Many species have already altered their distributions to more poleward and upslope regions because of increasing temperatures (Parmesan and Yohe, 2003; Hickling *et al.*, 2006; Parmesan, 2006; Lenoir *et al.*, 2008; Chen *et al.*, 2011). However, species-specific range expansion results in asynchronous colonization of new habitats by different species (Parmesan, 2006). Therefore, environmental variation due to climate change is predicted to largely affect ecological and evolutionary trajectories of species, resulting in biodiversity loss due to diminishing suitable habitats (Parmesan, 1996, 2006), population mismatches between predators and prey (Harrington

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et al., 1999; Durant *et al*., 2007), or between herbivorous insects and their host plants (Singer and Parmesan, 1993), including impact of pest insects on plants. Global change effect should therefore be measured across complex community-level interactions (van der Putten *et al*., 2004; Tylianakis *et al*., 2008; Berggren *et al*., 2009; Jamieson *et al*., 2012).

Since the colonization of land by plants, about 500 million years ago, plants and insects have engaged in an evolutionary arms race that has been the source of major diversification events and has resulted in plants and their herbivore insects covering more than half of the biodiversity described today (Strong *et al*., 1984). The arms race between plants and insects has led to the evolution of plant mechanisms to minimize damage by insects (Mitter *et al*., 1991; Futuyma and Agrawal, 2009a), including the deployment of chemical and physical defence traits (Schoonhoven *et al*., 2005). Insects have responded by evolving detoxification mechanisms (Feyereisen, 1999; Karban and Agrawal, 2002), behavioural avoidance mechanisms (Dussourd and Denno, 1991) and temporal and spatial specialization on different plant organs (Jaenike, 1990).

Rapid changes in the Earth's atmosphere initiated by human activity, including the use of fossil fuels, is resetting the spatial and ecological equilibrium of those complex co-evolutionary relationships, not only between plants and herbivores but also between plants and their mutualistic partners, including pollinators, and herbivores' predators (Coley, 1998). Specifically, CO_2 concentration in the atmosphere has risen from about 280 μl/l during preindustrial times to the current 397 μl/l and, at current rates of fossil fuel combustion, the atmospheric CO_2 concentration is predicted to double relative to the preindustrial level toward the end of the 21st century (IPCC, 2007). This increase in CO_2 is not only directly influencing the rates of photosynthesis and the carbon cycle but also is causing an unprecedented rate of planetary warming. Global average temperature has already increased by 0.8°C, and at current rates of fossil fuel use, global mean temperature is predicted to rise by 4°C by the end of the century (Solomon *et al*., 2009). Therefore, both plants and herbivores will experience dramatic changes in their niches within a very short period.

Although migration into more suitable habitats or shifts in phenologies have contributed historically to the maintenance of plant species during climate change, the current rate of climate change, combined with the effects of habitat fragmentation, has been shown to surpass many species' abilities to track the habitat to which they are currently adapted (Davis and Shaw, 2001; Davis *et al*., 2005; Pearson, 2006). To survive, plant species will therefore have to evolve or acclimate faster in order to cope with the new challenges provided by this new environment (Aitken *et al*., 2008; Anderson *et al*., 2012), including when facing novel and unprecedented higher rates of herbivore and pathogen attack (Coley, 1998).

Contrary to plants, herbivorous insects do not respond directly to changes in atmospheric CO_2 (Guerenstein and Hildebrand, 2008) but, given their ectothermic nature, temperature will be the major abiotic driver of their life cycle, population dynamics and geographic distribution (Bale *et al*., 2002). As a direct consequence, climate change is therefore expected to increase herbivory pressures in regions with a previously much lower impact of herbivores (Jepsen *et al*., 2008; Eskildsen *et al*., 2013), with detrimental consequences on natural plant populations (Jepsen *et al*., 2008) or crops (Thomson *et al*., 2010).

Evolution can proceed rapidly (Grant and Grant, 2002; Hairston *et al*., 2005; Agrawal *et al*., 2012), but we know very little about the evolutionary forces driving plant–herbivore interaction during climate change. Theoretically, adaptation could keep pace with novel threats, such as when plants from higher elevations or latitudes will be attacked by novel herbivore species, as long as they can maintain high genetic variation, individual fitness and effective population size (Aitken *et al*., 2008). But, will adaptive plasticity and/or evolution allow plant species to alter their phenotypes fast enough to persist during the fast invasion of novel herbivore communities (Loarie *et al.*, 2009)? What are the evolutionary constraints that will affect plant species adaptation to new habitats and new communities? This chapter highlights recent studies on how plants respond plastically or adapt to predicted future climate change scenarios, as well as phylogenetic constraints that might affect how plant and herbivores will impact each other under future conditions.

To address these questions, we focus specifically on studies along elevation gradients because environmental variables such as temperature, length of the growing season and water availability change dramatically and predictably along elevation gradients, which can result in consistent patterns of adaptation to local climatic conditions (Körner, 2007). Therefore, it is advantageous to exploit natural climatic variation along elevation gradients to explore adaptation in the context of global change (Etterson and Shaw, 2001; Kremer *et al.*, 2012). Additionally, compared to much larger-scale latitudinal gradients, elevation gradients minimize the confounding effects of historical and biogeographical differences in, for instance, plant and herbivore species pools (Hodkinson, 2005). Along elevation gradients, shifts in abiotic and biotic conditions promote turnover in plant and insect strategies in communities, including plant defence strategies and herbivore host plant choices (Pellissier *et al.*, 2010, 2012).

3.2 Herbivore Abundance and Plant Defences Along Elevation Gradients

Because insects are ectotherms and thus require external heat for their development (Hodkinson, 2005), insect abundance generally decreases with lower temperatures at higher elevation (Pellissier *et al.*, 2012). Therefore, the pressure of insect herbivores on plants is also reduced in highlands compared to lowlands (Hodkinson, 2005; Pellissier *et al.*, 2012; Rasmann *et al.*, 2013). According to plant defence theory, plants inhabiting high elevations should consequently relax their defence syndrome compared to their lowland living relatives (Coley and Barone, 1996; Coley, 1998; Pellissier *et al.*, 2012). Indeed, when measuring resistance against a generalist herbivore across 16 congeneric pairs of high- versus low-elevation species, we found that caterpillars grew larger on high elevation species overall (Pellissier *et al.*, 2012). Defence variation between high and low elevation also occur within species. Populations of *Plantago lanceolata* from high elevation had lower constitutive and induced production of secondary metabolites when compared to low-elevation populations (Fig. 3.1). However, a recent meta-analysis investigating the variation of plants' defences along

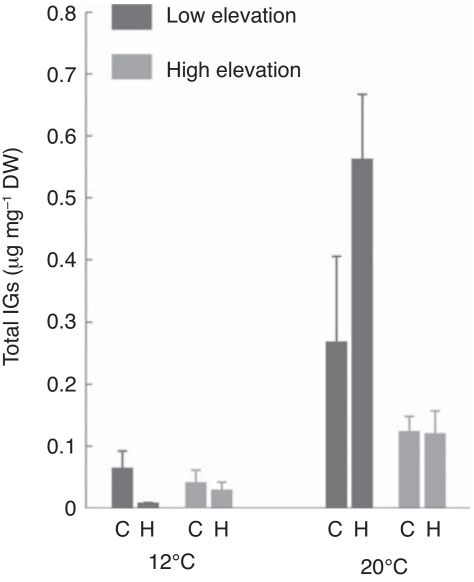

Fig. 3.1. Effect of temperature on plant defences. Shown are the means (±1 SE) of iridoid glycoside (IG) production of high (1500 m above sea level (asl)) and low (500 m asl) elevation ecotypes of *Plantago lanceolata* plants grown at 20°C or 12°C. These temperatures correspond to average conditions at 500 and 1500 m asl, respectively. Plants were further left undamaged (C) or were induced for 4 days with the generalist caterpillar herbivore (*Spodoptera littoralis*) (H). Ecotypes from high elevation express a genetically based reduction in iridoid glycoside production. Additionally, temperature inhibits induction after herbivory on both ecotypes. (Adapted from Pellissier *et al.*, 2014).

elevation gradients indicated that the decrease in plant defence was not universal, as increases in the concentration of phenol-based molecules with increasing elevation had also been documented (Rasmann *et al*., 2013).

Plants' investment in allelochemicals is predicted to be the outcome of synergistic interactions between biotic and abiotic factors (Coley and Barone, 1996). For instance, we have recently discovered that *P. lanceolata* constitutive production and deployment of iridoid glycosides after herbivory is lower in colder temperature conditions (Fig. 3.1). On the contrary, higher levels of phenolic compounds, which deter insect feeding and reduce herbivore densities (Forkner *et al*., 2004), can protect the leaves of high-elevation plants from photodamage by acting as antioxidants (Close and McArthur, 2002). Similarly, leaves that have high concentrations of cellulose and lignin (i.e. fibre) are stronger, and potentially longer-lived, at high-elevation sites than leaves with low fibre concentrations, and at the same time are more resistant against herbivore damage (Abrahamson *et al*., 2003; Richardson, 2004). Additionally, the 'resource availability hypothesis' (Coley *et al*., 1985; Endara and Coley, 2011) suggests that plants adapted to resource-poor and stressful habitats are predicted to be relatively slow-growing, have low tolerance for herbivory and thus should invest heavily in defences. Indeed, we have recently found that high-elevation ecotypes of *Vicia sepium* produce lower levels of ant-attractive volatile organic compounds (VOCs) compared to low-elevation ecotypes, but induction by the wound-related hormone, jasmonic acid, increased VOC production to similar levels across the elevation range (Fig. 3.2). As a consequence, a reduction in herbivory pressure toward higher elevation alone does not lead forcedly to a decrease in plant defences (Schemske, 2009), but defensive traits might respond differently to the variation in herbivore pressure and abiotic factors, and this is expected to vary among plant clades. It is therefore challenging to predict which species is preadapted to a shift in herbivory following climate change.

Under the scenario of increasing temperature, it is expected that insect abundance and diversity will increase at higher elevation (Pellissier *et al*., 2012; Rasmann *et al*., 2013). Indeed, the best-documented examples of species migration from recent climate change are for animals, while plants show reduced responses, especially along latitude (Chen *et al*., 2011). As a consequence, climate change will cause disequilibrium between the current co-distribution of plant and insects. Asynchronous

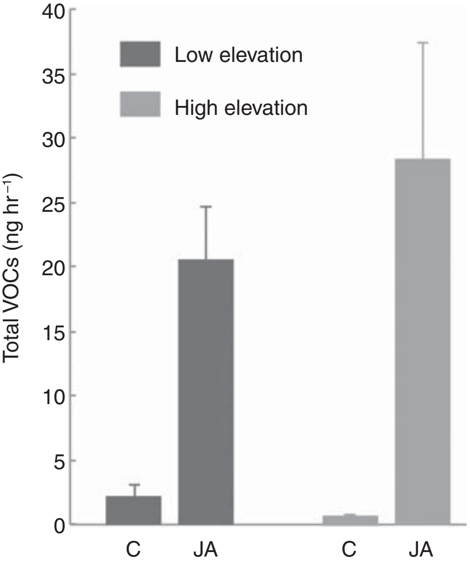

Fig. 3.2. Interaction between constitutive and inducible defences along elevation gradients. Shown is the overall mean (±1 SE) production of volatile organic compounds (VOCs) from the bush vetch, *Vicia sepium*, ecotypes that were either left undamaged (C) or induced by exposing the plants to methyl jasmonate (JA). Seeds of different ecotypes were collected at 500 m asl (low elevation) or at 1700 m asl (high elevation). Low-elevation ecotypes had higher constitutive levels of VOC production, but induction increased it to similar levels for both ecotypes (i.e. ecotype × induction interaction, $P < 0.05$). These results are thus indicative of physiological negative correlations (or trade-offs) among different defence strategies, such as between the constitutive and the inducible production of VOCs. (Adapted from Rasmann *et al*., 2014).

colonization of high elevation between insect and plants will shape novel interactions, as more abundant and diverse insect herbivore fauna will come across an alpine flora that has evolved in low herbivory conditions (Rasmann *et al*., 2013). We might therefore speculate that climate change will impose strong fitness consequences on plants occurring at higher elevation or latitude. Nevertheless, the consequences of increased herbivory at high elevation are ultimately the function of the current plants' defence abilities, and their potential for plastic and adaptive response to resist insect natural enemies.

3.3 Phenotypic Responses, Adaptation and Evolution during Climate Change

Adaptive phenotypic plasticity enables species to cope with spatially and temporally heterogeneous environments, such as when plants are under different climates or are colonized by new herbivore species. Several examples show that plant defensive traits can respond plastically to variation in CO_2 or temperature in which higher concentrations of CO_2 or temperature alter both plant chemistry and morphology (reviewed in DeLucia *et al*., 2012; Zavala *et al*., 2013). The modulation of plant responses against herbivore attack is mediated by the complex signalling of the hormonal network (Howe and Jander, 2008), and current data suggest that exposure to either elevated CO_2 or high temperatures indeed alters hormonal signals in a predictable fashion (DeLucia *et al*., 2012). For instance, the antagonistic interaction between the wound-inducible hormone, jasmonic acid (JA), and the pathogen-inducible hormone, salicylic acid (SA) (Thaler *et al*., 2012), is more evident under elevated CO_2, which downregulates JA (and ethylene (ET)) pathways and increases susceptibility to herbivore attack (Casteel *et al*., 2008, 2012a,b; Zavala *et al*., 2008). On the other hand, higher-than-average temperatures, instead of driving antagonistic interactions among phytohormones, have been shown generally to stimulate the production of JA, SA and ET, which has resulted in increased levels of allelochemicals and plant resistance to both pathogens and herbivores (Maimbo *et al*., 2007; Arimura *et al*., 2009; Clarke *et al*., 2009; Mosolov and Valueva, 2011). These findings are in line with our work showing that colder temperatures inhibit the constitutive production and the induction of defences along elevation gradients in *P. lanceolata* (Fig. 3.1). Therefore, the temperature-driven upregulation of hormones, and subsequent higher induced resistance, could reduce the susceptibility of plants to herbivore attack produced by elevated CO_2 alone (Niziolek *et al*., 2013).

Recent evidence is also showing that phenotypic plasticity induced by herbivore or pathogen attack can also occur across generations (i.e. transgenerational plasticity), in which previous parents' experience of biotic and abiotic stressors influences resistance trait expression in the offspring (Bonduriansky *et al*., 2012). Transgenerational plasticity is defined as the transmission of epigenetic variation, which is mediated by DNA methylation, and changes in chromatin structure, and RNA expression. Plants can face more fluctuating and more severe environments by passing on the memory of abiotic stressors such as heat, frost and drought (reviewed in Walter *et al*., 2013). For instance, the F_3 generation of *Arabidopsis thaliana* plants exposed to heat stress performed better when their parents were also exposed to high temperature. This is not true, however, when imposing a cold treatment (Whittle *et al*., 2009). Nevertheless, these findings indicate that plants can cope with rapid changes in the environment with non-permanent but heritable epigenetic mechanisms. Indeed, natural epiallelic variation has been tied to ecologically relevant phenotypic plasticity in *Viola cazorlensis* (Herrera and Bazaga, 2010). Furthermore, in laboratory experiments, both insects and pathogens can increase resistance to insect herbivores and pathogens in the next generation of plants via epigenetic heritable modifications of the genome (Slaughter *et al*., 2011; Luna *et al*., 2012; Rasmann *et al*., 2012a). Therefore, transgenerational-induced resistance could play an important role when plants colonize new environments, in which plants will suffer drastic bottlenecks that reduce genetic diversity. Climate change might favour increased variation at the level of the epialleles, thus favouring faster adaption and evolution into the new environment (Latzel *et al*., 2012; Rasmann *et al*., 2012b; Zhang *et al*., 2013). Nevertheless, the study of epigenetics in natural populations is in its infancy, and it is currently unknown to what extent epigenetic modulation may help species cope with the interactive effects of CO_2, temperature and herbivore increases during climate change.

In addition to phenotypic plasticity and epigenetic variation, plants are expected to evolve increased resistance when faced with novel threats. A recent study indicates that defence evolution and tolerance may happen over a short timescale of a few generations when under strong selection (Agrawal *et al*., 2012). Therefore, rapid evolution events, coupled with phenotypic plasticity, may play an important role in species response to increased herbivory rates under climate change (de Sassi and Tylianakis, 2012), as long as standing genetic and epigenetic variation, individual fitness and large enough population size are maintained (Aitken *et al*., 2008; Hoffmann and Sgro, 2011). Alternatively, adaptation will lag behind climate change, creating a mismatch between optimal phenotypic values in the current environment and the suboptimal values in the new environment (Etterson and Shaw, 2001; Davis *et al*., 2005; Shaw and Etterson, 2012).

Therefore, not solely the ability for evolving traits that increase fitness under new conditions but also the speed of evolution will be an essential factor determining whether a species is able to adapt to climate changes. Finally, for species spanning various ecological conditions, migration, gene flow and population admixture could facilitate adaptation by introducing adapted alleles (e.g. for increased resistance) into populations that are locally adapted to a set of abiotic or biotic conditions (Anderson *et al*., 2012).

3.4 Phylogenetic Distribution of Plant Resistance and Potential Adaptive Response

Predicting how and when adaptive evolution might rescue species from climate-induced ecological changes is a very difficult challenge, as current rates of climate change are unprecedented in historical records. Increasing evidence supports rapid evolution in response to environmental change potentially influencing species' demographic responses to those drivers (Gienapp *et al*., 2008). Therefore, studies estimating the defence evolution potential in species, which may happen over a short time frame, are greatly needed to assess the evolution potential against the shift in ecological conditions (Agrawal *et al*., 2012). One approach to investigate evolution potential is to use microevolutionary experiments and estimate the selection and heritability of target traits across generations (e.g. Visser, 2008; Sinervo *et al*., 2010). However, this approach is highly time-consuming and thus difficult to apply to a large number of species simultaneously. In contrast, phylogenetic inferences of past rates of niche evolution may provide relevant information on the evolution potential of a given lineage (Pearse and Altermatt, 2013). Recently, Lavergne *et al*. (2013) showed that the likelihood of demographic decline was associated with the slow rate of past niche evolution within a given clade. Rates of past evolution of ecological requirement obtained from phylogenetic analyses thus provide relevant information to investigate the consequence of climate change on species' fate (Araujo *et al*., 2013; Quintero and Wiens, 2013).

Phylogenetic data have increasingly been used in the study of plant defences over the past decade (Mitter *et al*., 1991; Futuyma and Agrawal, 2009a). For instance, phylogenies have been used in comparative analyses to investigate the evolution of plant secondary metabolite compounds and resistance within a clade (Johnson *et al*., 2009; Rasmann and Agrawal, 2011; Campbell and Kessler, 2013), assess the role of defence evolution in species radiation (Farrell *et al*., 1991; Agrawal *et al*., 2009a), or in species coexistence (Becerra, 2007; Kursar *et al*., 2009). A recurrent pattern emerging from phylogenetic studies of plant phenotypes is that strategies tend to be clustered phylogenetically, i.e. defensive traits are more similar between closely related taxa than when species are drawn randomly from the phylogeny (i.e. phylogenetic conservatism) (Wiens and Penkrot, 2002). This pattern is usually interpreted to be a consequence of shared ancestral characters leading related species to respond similarly to the same shift in ecological condition (Wiens *et al*., 2010). The conservatism and lability of a trait within a phylogeny may therefore provide information on the rate of evolution in the past for a given clade. A clade of closely related species displaying a large variation in a trait indicates that this trait may shift rapidly either through phenotypic plasticity or evolution (Lavergne *et al*., 2013). Rates of niche evolution could, in turn, provide information on the evolution potential of a clade to adapt to novel ecological conditions. But, the link between potential evolution and past rates of defence evolution has remained virtually unexplored so far (Futuyma and Agrawal, 2009a).

Phylogenetic studies that measure the evolution of ecological preferences have revealed various rates of evolution among clades (Litsios *et al*., 2012; Kostikova *et al*., 2013), but no studies have yet applied this concept in the study of plant defences. Higher rates of the past evolution of defences would reflect high evolutionary potential within populations, possibly because the genetic mechanisms that promote defences can be easily modulated. Such lineages, having experienced relatively rapid evolution of defences in the past, would thus be able to adapt better to changing herbivory rates than others. Here, we illustrate this approach using a data set of *Asclepias* species and their induced toxic cardiac glycoside (or cardenolide) production (Agrawal *et al*., 2009a). We applied a recently developed method that uses Bayesian inference to sample phenotypic evolutionary rates, implemented in the R package (Eastman *et al*., 2011). This approach models rate heterogeneity in a Bayesian framework by using a reversible-jump Markov chain Monte Carlo (MCMC) approach (Eastman *et al*., 2011). The outcome is a posterior distribution of evolutionary rates for each branch in the phylogeny. Applied to cardenolide production in *Asclepias* species, this analysis illustrates how the past rate of defence evolution differed among clades. The Incarnata clade showed a higher modularity of both constitutive and induced defences, and suggested that the ability to shift defence had phylogenetic inertia, contrary to the Syriaca clade (Fig. 3.3).

Some phylogenetic groups are thus expected to be more flexible and likely to shift defence strategies to cope with novel challenges under climate change. However, the study of defence evolution using phylogenies is currently restricted to a few plant clades (Agrawal *et al*., 2009a; Becerra *et al*., 2009; Johnson *et al*., 2009; Kursar *et al*., 2009; Pearse and Hipp, 2012; Campbell and Kessler, 2013). Future research should focus on the evolution of defence strategies in broader phylogenetic groups. However, given the complexity in secondary metabolites produced by the plant as a defence mechanism, novel methodological approaches involving broad-scale metabolite identification, bioassay with herbivores and quantitative genetic studies for measuring selection on metabolite production, coupled with broad-scale comparative phylogenetic analyses, should be developed to address fully and disentangle the biotic and abiotic drivers and phylogenetic constraints on plant defence evolution (Rasmann and Agrawal, 2009) and how global climate change might affect it.

While the overall abundance of insects is expected to increase at high elevation, imposing more severe pressure on plant communities (Rasmann *et al*., 2013), the species-specific response of insects to climate change is expected to be idiosyncratic. We recently showed that the phylogenetic composition of insect herbivores (Lepidoptera) along the elevation gradient was shaped by the diversity of host plant lineages in the community (Pellissier *et al*., 2013). Butterflies are recognized to have radiated through the colonization of novel host plant clades followed by bursts of diversification (Ehrlich and Raven, 1964; Fordyce, 2010), and indeed, most butterfly taxa are often associated with particular plant clades (Janz and Nylin, 1998; Menken *et al*., 2010) by being able to detoxify clade-specific plant secondary metabolites. As a consequence, variation in the availability of plant lineages in space implies a shift in trophic niches available for specialized butterflies. In addition, high-elevation herbivores tend to be more generalistic, given

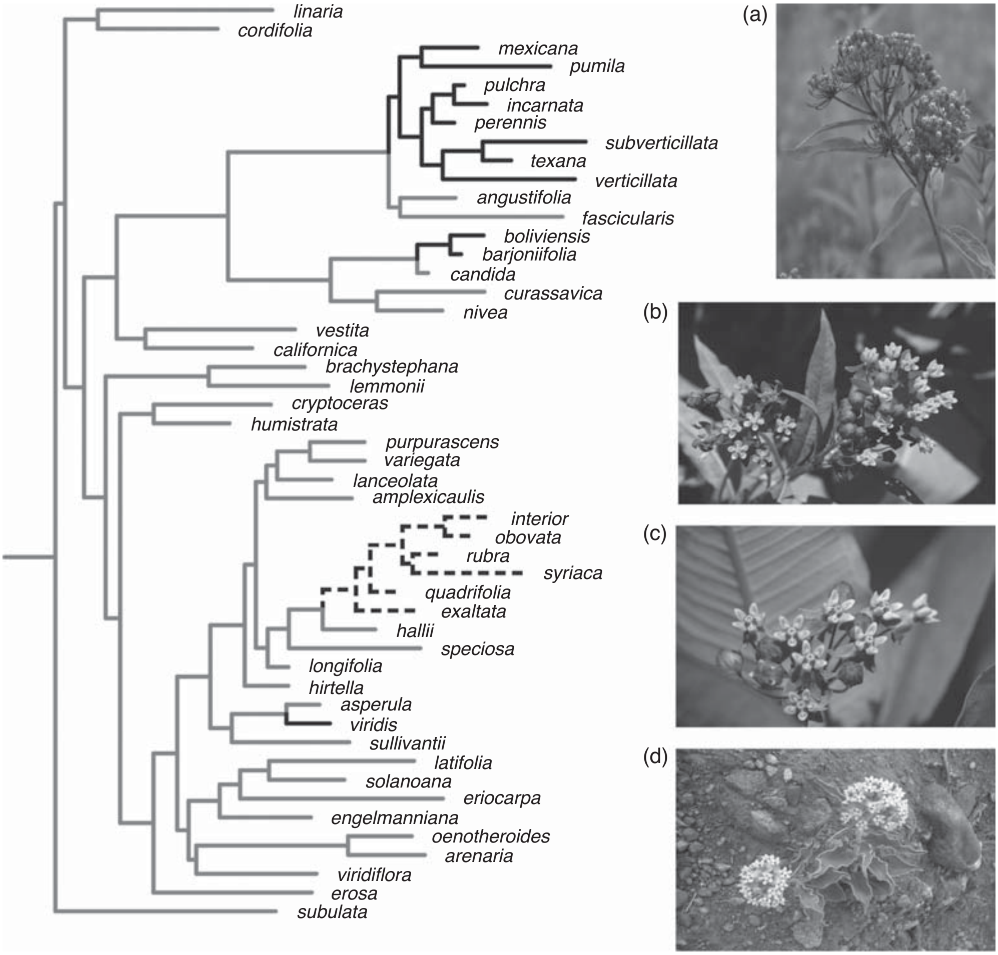

Fig. 3.3. Phylogenetic analyses on the rate of defence evolution. Shown is a pruned phylogeny of the *Asclepias* genus redrawn after Fishbein *et al*. (2011) and Rasmann and Agrawal (2011). The branches of the phylogeny are drawn according to their rate of defence evolution based on the average constitutive and inducible production of toxic cardiac glycosides (or cardenolides) for each species. Black lines with different patterns show either lower (dotted black lines) or higher (solid black lines) than the median posterior estimate of evolutionary rate across the tree. Shown are representative species of *Asclepias*: (a) the swamp milkweed, *Asclepias incarnata*; (b) the tropical milkweed, *Asclepias curassavica*; (c) the common milkweed, *Asclepias syriaca*; and (d) the desert milkweed, *Asclepias erosa*. In the text, we argue that the Incarnata clade, for instance, has higher chances of shifting to a different defensive phenotype when placed into a new herbivore environment, which could be imposed by climate change, than the Syriaca clade. (Photographs (a) and (c) courtesy of Sergio Rasmann; (b) and (d) courtesy of Cristian Villagra.)

their opportunity to feed on less defended plants (Pellissier *et al*., 2012). Under climate change, shift in abiotic conditions and herbivory pressure is expected to favour some plant lineages over others, according to their potential for adaptation. In turn, it should rearrange the current equilibrium in defence-mediated composition of plant–herbivore communities. As a consequence, climate change may impact plant–herbivore communities along the elevation via complex feedback mechanisms.

3.5 Evolutionary Traits' Correlations and Trade-offs

The evolutionary rescue of endangered populations due to climate change may be hampered by covariation among traits, which may cause species' niches to be conserved over time. A plant's defence arsenal against herbivore attack is multimodal and highly diverse, and plant defence syndrome is the outcome of synergistic and antagonistic integrations at the plant physiological level (Agrawal and Fishbein, 2006; Agrawal *et al*., 2009b) and their emerging ecological properties (Kursar and Coley, 2003; Kursar *et al*., 2009). Because plants, as with all organisms, are constrained by the amount of resources they can allocate to different traits, trade-offs among defence and growth (Herms and Mattson, 1992), among tolerance and defence (Strauss and Agrawal, 1999), and among defensive traits such as between direct and indirect defence (Ballhorn *et al*., 2008), or between constitutive and inducible defences (Thaler and Karban, 1997; Heil *et al*., 2004; Rasmann *et al*., 2009) have all been postulated and observed. For instance, trade-offs among the constitutive and inducible mode of deployment of the same defence traits may be clearly predicted, since the precursors and the molecular building blocks are exactly the same; thus, they should come from the same source. Alternatively, traits may show negative correlations due to adaptation, in which traits might show what appears to be a trade-off if they are ecologically redundant and costly (Agrawal *et al*., 2010). None the less, trade-offs in defence are rarely found (Koricheva *et al*., 2004) and simultaneous deployment of alternative strategies may provide redundancy or 'reinforcement' for enhanced protection (Rasmann and Agrawal, 2009).

As mentioned above, a classic example of expected trade-off among defensive traits should result among constitutive and inducible resistance (Rasmann *et al*., 2009). We are not aware of studies that directly tested the climate change effect on defensive trait correlations, but our recent investigations are showing variation in constitutive and inducible release of VOCs along elevation gradients. In the European Alps, *V. sepium* plants grow from lowlands up to about 2200 m above sea level. When measuring VOCs in high- versus low-elevation genotypes, we found that low-elevation genotypes produced higher levels of constitutive VOCs but high-elevation genotypes were more inducible, indicating potential elevation-mediated trade-offs in indirect defence deployment (Fig. 3.2). Similarly, across 18 species of pines (*Pinus* spp.), constitutive production of resins and phenolics increases at higher latitudes and altitudes, and with the coldest temperatures, whereas inducibility of those defences increases toward the equator (Moreira *et al*., 2014). Therefore, climate acts as a key driver of defence profiles, their expression, and in turn is mediated by the constraints imposed by trade-offs. Future research is thus needed to measure the interactive effect of temperature and CO_2 on defensive trait correlation and trade-offs.

3.6 Concluding Remarks and Future Directions

Plants' responses to predicted increases in herbivory during climate change will be the outcome of genetic and epigenetic variation, phenotypic plasticity and the rate of adaptation. In Fig. 3.4, we summarize the adaptive and selective mechanisms by which plants might respond to increased damage by herbivores, as discussed in the text. However, while the defence mechanisms and pathways are largely known for a few model plant species, the overall diversity of defences across the plant tree of life is largely unknown, which may limit our ability to predict the outcome of novel plant–insect interactions under climate change. Future studies of plant defence should focus on unravelling the diversity of defence mechanisms at broad phylogenetic scale.

Finally, several reports on global warming and elevated CO_2 manipulations have illustrated their interacting effects on plant and animal development rates, host quality, phenology, voltinism patterns and ecological interactions (DeLucia *et al*., 2012), and one aspect that we have not considered in this chapter is that the populations of many insect herbivores are regulated strongly by invertebrate predators. Top-down regulation by predators and parasitoids of herbivore insects is also affected by climate change (Hance *et al*., 2007; Berggren *et al*., 2009; de Sassi *et al*., 2012; de Sassi and Tylianakis, 2012; Henri *et al*., 2012). Therefore, future work should take into account the interactive effect of bottom-up direct plant defences and the top-down effect of predators mediated by plant indirect defences, which is particularly important when trying to predict insect pest pressure on crop fields in a warming climate.

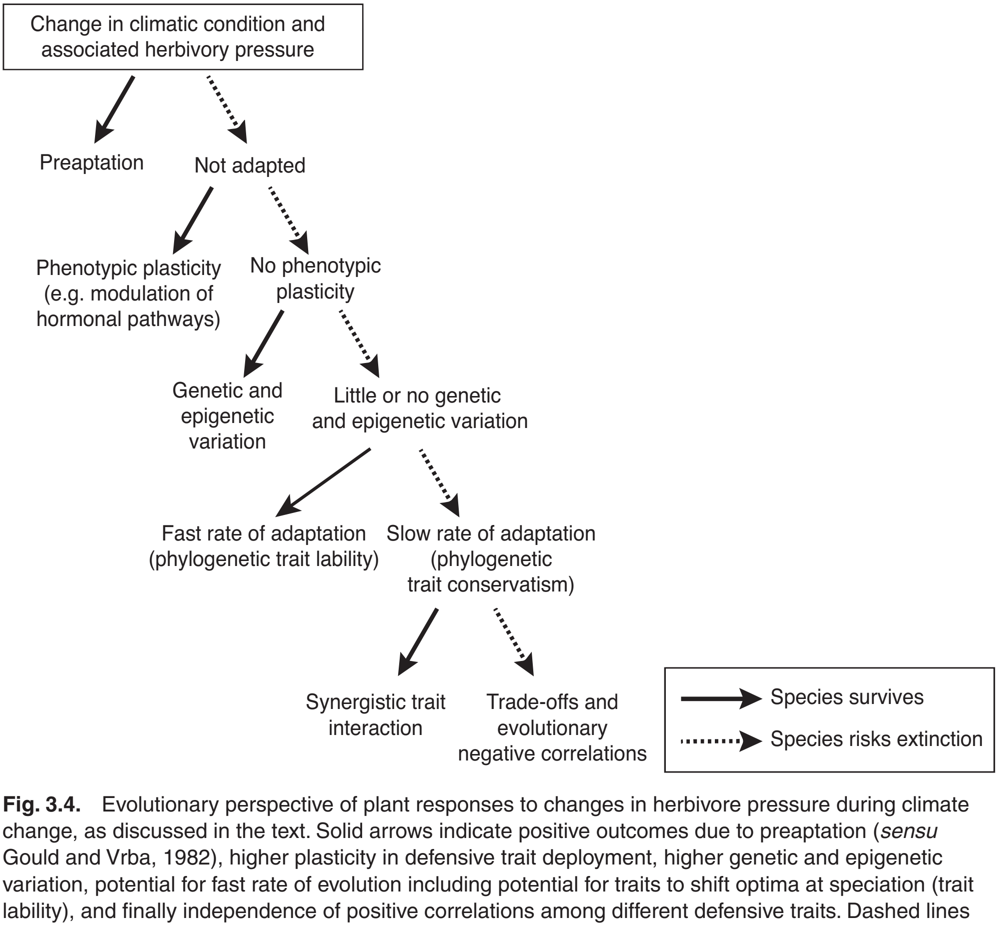

Fig. 3.4. Evolutionary perspective of plant responses to changes in herbivore pressure during climate change, as discussed in the text. Solid arrows indicate positive outcomes due to preaptation (*sensu* Gould and Vrba, 1982), higher plasticity in defensive trait deployment, higher genetic and epigenetic variation, potential for fast rate of evolution including potential for traits to shift optima at speciation (trait lability), and finally independence of positive correlations among different defensive traits. Dashed lines represent micro- and macroevolutionary constraints opposite to those described above.

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4

Boreal Woody Species Resistance Affected by Climate Change

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Abstract

Climate change undoubtedly affects the metabolism and resistance of woody plants, and results in changes in their competitive management. Due to low climatic niche evolution, trees and shrubs are slow to react to climate change. In addition, current studies show rather variable results. Therefore, difficulties arise in finding unanimity concerning the impacts of climate change on woody species growth, secondary metabolism and their relationships with other organisms. Here, we review the literature based on current results of the main climate change factors, including increased CO_2, temperature and ultraviolet radiation. We summarize the interactions of woody plant growth with defensive metabolism, with a special focus on simultaneously affecting changes.

4.1 Introduction

Atmospheric CO_2, temperature and UVB levels have been increasing since the industrial revolution (e.g. Fowler *et al.*, 1999). According to the Intergovernmental Panel on Climate Change (IPCC, 2013), atmospheric greenhouse gases have changed global climate by increasing surface temperature by 0.85°C during the period from 1880 to 2012. This is due mainly to increased concentration of CO_2 to more than 390 ppm (Tans, 2012), and in the near future, the increase in CO_2 concentrations are suggested to be higher and even faster (Peñuelas *et al.*, 2013). Atmospheric CO_2 level is estimated to double by 2100, accompanied by a 0.3–4.8°C increase in annual temperatures on a global scale (IPCC, 2007). Climate change factors and other environmental factors (aerosol concentration, pollutants, clouds, surface reflectance, etc.) also interplay with UV radiation, causing a potential delay in the recovery of the stratospheric ozone layer and modifying the level and spectral quality of UV radiation incident on the Earth's surface.

The chemical resistance of woody species to environmental changes is an utmost important trait for plant growth and survival. The allocation of available resources to defensive needs is determined mostly by a plant's genetic pool, modified by plant phenology and ontogeny (e.g. Jamieson *et al.*, 2012). However, keeping a continuously high constitutive level of defence, and also induction of these responses to a multitude of signals, is costly, resulting in trade-off phenomena (i.e. change in the balance of carbon/energy allocation between growth and defence) in plant tissues (e.g. Bryant *et al.*, 1983; Herms and Mattson, 1992; Gerzhenson, 1994). Climate change factors such

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as elevated temperature, UVB radiation, CO_2, water conditions and concomitant changes in soil quality are elementary factors that cause plant stress, with accompanying changes in defence strategies.

Plants utilize a wide array of mechanisms to buffer and protect themselves against biotic (such as viral, bacterial, fungal pathogens and herbivores) and abiotic (e.g. CO_2, temperature, UVB, drought) stressful changes in environmental conditions. Anti-stress mechanisms of plants include structural (such as thick epidermis, tough epidermis, thick cuticula, spines, trichomes, hairs) and phytochemical defences (different bioactive compounds). Several phytochemicals that take part in plant defence also perform important plant physiological functions, for example interaction with mycorrhiza, or they may affect soil quality by modifying litter decomposition (Fischer *et al.*, 2006; Schweitzer *et al.*, 2008). Plant defence responses are often multi-component, indicating that there are multiple and apparently complementary defence responses involved (e.g. Tuzun and Bent, 1999), or they can be multifunctional, meaning that the same component, and in addition to its decomposition products produced during the defence reactions, all have defensive roles (e.g. Rowell-Rahier, 1984; Julkunen-Tiitto and Meier, 1992).

The main classes of phytochemical defences are terpenoids, phenolics and alkaloids, covering tens of thousands of compounds identified so far. The terpenoids, originating from isoprene units, are classified into seven groups based on molecular size. They are found in higher concentration, especially in essential oils and resins (e.g. Gerzhenson, 1994). Higher molecular weight terpenoids have a bitter taste and are even toxic, while highly volatile monoterpenoids are mostly pleasant smelling and found to be dominant compounds in the volatile blends emitted by plants (e.g. Guenther *et al.*, 1995; Kesselmeier and Staudt, 1999; Lindfors and Laurila, 2000). Phenolics are quite universal in higher plants, found in all plant tissues, and most have antimicrobial activity, a bitter taste, and may even be toxic. They can range from simple and low molecular mass phenolics up to higher molecular mass polymeric ones, such as tannins. Alkaloids, nitrogen-containing compounds, form the largest and most diverse group of compounds found in vascular plants. Most of them have high (toxic) or moderate (bitter-tasting) activity and are generally found in low concentrations in roots, leaves and fruit (Stermitz *et al.*, 1994; Seigler, 1998; Virjamo *et al.*, 2014). For instance, a wide range of piperidine alkaloids that vary from 0.03% to 0.08% of the fresh weight is found in conifers (Tawara *et al.*, 1993; Virjamo *et al.*, 2014).

The level of defences in plant tissues are dependent on plant age, phenology and ontogeny, as well as on environmental conditions such as temperature, light quality and nutrients (e.g. Stermitz *et al.*, 1994; Julkunen-Tiitto *et al.*, 1996; Keinänen *et al.*, 1998, 1999a; Graglia *et al.* 2001; Laitinen *et al.*, 2002; Keski-Saari and Julkunen-Tiitto, 2003a,b; Glynn *et al.*, 2004; Laitinen *et al.*, 2005; Nyman and Julkunen-Tiitto, 2005; Stark *et al.*, 2007). Generally, genotype-dependent defences are found in constitutive levels, while many of the changes are also found to be inducible (e.g. Keinänen *et al.*, 1999b; Laitinen *et al.*, 2000, 2004; Nyman and Julkunen-Tiitto, 2000; Roitto *et al.*, 2003; Huttunen *et al.*, 2008; Gerson *et al.*, 2009; Ruuhola *et al.*, 2011; Virjamo and Julkunen-Tiitto, 2014) and are widely assumed to be accompanied by the overall ecological costs to the plants (e.g. Herms and Mattson, 1992; Cipollini *et al.*, 2003). The turnover rate of the compounds may be very high, such as for monoterpenes, kaempferol-glycosides (e.g. Strack *et al.*, 1989; Gerzhenson, 1994), or then nearly absent, such as for salicortins, papyriferic acids, condensed tannins, which also indicates variable maintenance costs for plants (e.g. Tahvanainen *et al.*, 1991; Julkunen-Tiitto *et al.*, 1996; Mutikainen *et al.*, 2002).

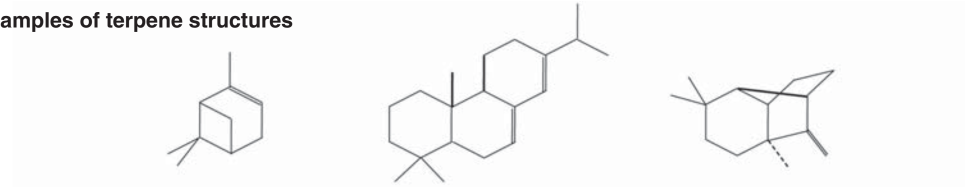
Here, our main focus is how the anti-stress defences of deciduous and coniferous boreal woody species are affected by changes in CO_2, temperature and UVB, and by combinations of changes in these factors. Anti-stress defences in boreal species are mainly compounds that are constitutively present in high or moderately high concentrations in tissues, such as phenolics or triterpenes (Fig. 4.1). Condensed tannins are the most abundant constitutive phenolics in all boreal species, while different flavonoids, phenolic acids and phenolic glycosides are found in variable amounts in species and specific plant parts. The volatile piperidine alkaloids are widespread in low concentrations in conifers, but still little studied (Fig. 4.1).

4.2 The Effect of CO_2 on Plant Defence

Over three decades, plenty of studies of the effects of CO_2 enhancement on plant species have been conducted either in greenhouses, field open-top, close-top chambers or open experimental fields. The proper experimental condition is one of the options inducing variation in defences and should be considered in the interpretation of responses (see, for example, Peltonen *et al.*, 2005). Generally, elevated CO_2 has been reported to increase plant growth and biomass accumulation (e.g. Ceulemans and Mousseau, 1994; Norby *et al.*, 1999; Noorments *et al.*, 2001; Paajanen *et al.*, 2011; Lavola *et al.*, 2014), while controversial effects on carbon-based plant defence compounds between tree species, genotypes, plant organs, duration of exposure and different soil conditions have been found (e.g. Lindroth *et al.*, 2001, 2002; Zvereva and Kozlov, 2006; Paajanen *et al.*, 2011; Nybakken and Julkunen-Tiitto, 2013; Lavola *et al.*, 2014). For example, Cole *et al.* (2010) showed that the growth of wild clones of *Populus tremuloides* increased an average of 53% over the past five decades when the ambient CO_2 concentration increased by 19.2%. This growth enhancement was dependent on plant moisture conditions and plant age, but not on the sex or location of the trees (Cole *et al.*, 2010). In addition to direct effects, enhanced CO_2 can affect plant defence indirectly; for example, via changes in physiological development and phenology (e.g. Jach *et al.*, 2001). Basically, increased carbon-based defences are claimed to be the result of higher photosynthetic carbon gain and carbon excess (e.g. Lambers, 1993). In a literature review of 17 plant species, about half of which were woody species, Peñuelas *et al.* (1997) showed that the CO_2 effect on carbon-based defensive compounds (phenolics and terpenoids) and the growth under low and high nutrient availabilities was highly variable, depending on species, plant age and duration of the experiment. At low nutrient level, a negative correlation between chemistry and growth was found, while under high nutrient level both growth and chemistry increased with elevated CO_2. Moreover, there were differences in responses between defensive compounds; larger responses were found in phenolics compared with terpenoids. Similarly, according to Zvereva and Kozlov (2006), based on meta-analyses of 31 plant species, including 18 woody species, and Stiling and Cornelissen (2007), based on 59 studies, elevated CO_2 increased phenolics, while there was no change in terpenes.

Accordingly, a low response of terpenoids to CO_2 has been reported in needles of 20-year-old *Pinus sylvestris* trees grown over 5 years in closed-top chambers (Räisänen *et al.*, 2008a). The long-term exposure of *P. sylvestris* increased the accumulation of condensed tannins, with a concomitant significant decrease in monoterpenes (nine compounds, of which alpha-pinene and delta-3-carene were the most abundant), while no changes in lower molecular weight phenolics (cinnamic acids, flavan-3-ols, flavonols, flavones, non-acylated and acylated flavonols) were found (Räisänen *et al.*, 2008a). Moreover, graphical vector analyses revealed no dilution effect, but preferably indicated a reduced biosynthesis of monoterpenes (Räisänen *et al.*, 2008a) in *P. sylvestris* needles. This is in agreement with the previous studies by Sallas *et al.* (2003): total monoterpenes and resin acids decreased due to elevated CO_2. Sallas *et al.* (2003) reported that the concentration of total phenolics in the needles of *P. sylvestris* seedlings had no significant change, while in the needles of *Picea abies* seedlings they were reduced in response to elevated CO_2. Kainulainen *et al.* (1998) have claimed that monoterpene

Examples of terpene structures

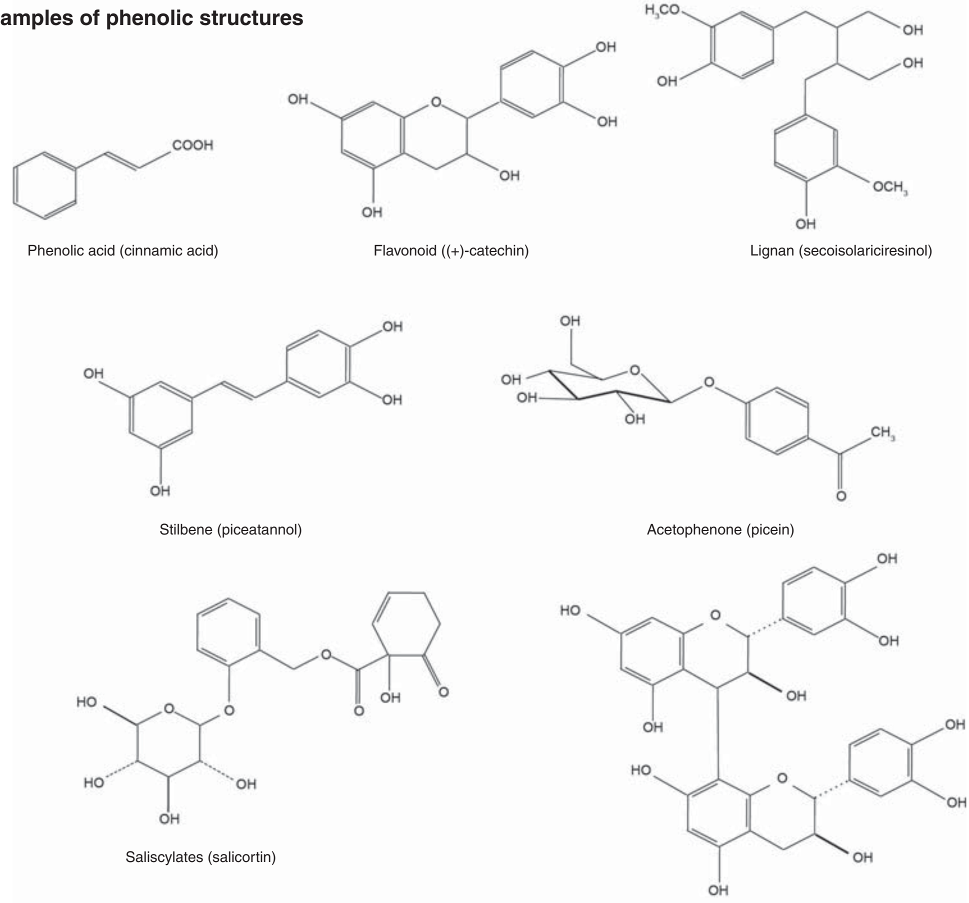


Monoterpene (pinene)

Diterpene (abietadiene)

Sesquiterpenene (longifolene)

Examples of phenolic structures



Phenolic acid (cinnamic acid)

Flavonoid ((+)-catechin)

Lignan (secoisolariciresinol)

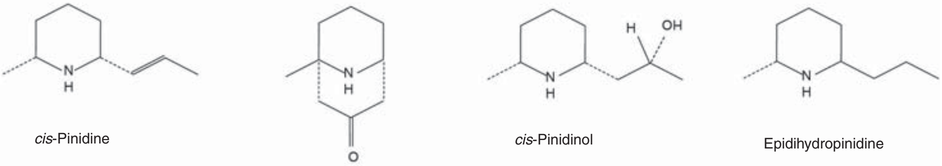
Stilbene (piceatannol)

Acetophenone (picein)

Saliscylates (salicortin)

Condensed tannin (procyanidin dimer)

Examples of piperidine alkaloid structures



cis-Pinidine

Euphococcinine

cis-Pinidinol

Epidihydropinidine

Fig. 4.1. Defensive compounds found in boreal plant species, such as *Betula* spp., *Salix* spp., *Pinus sylvestris* and *Picea abies*.

biosynthesis is strictly genetically controlled and only slightly affected by environmental change. Other non-consistent responses to elevated CO_2 in monoterpene emissions have also been reported for different species: increase in *Betula pendula* (Vuorinen *et al*., 2005) and no effect in the needles of old *P. sylvestris* individuals (Räisänen *et al*., 2008b).

Resembling molecular size biased responses are found in deciduous species. Increased atmospheric CO_2 (3 months exposure of 700 and 1040 ppm CO_2) decreased several dynamic phenolics (salicylates) in the leaves of greenhouse chamber-grown seedlings of *Salix myrsinifolia* and increased more static phenolics (condensed tannins), in addition to increasing total shoot biomass (Julkunen-Tiitto *et al*., 1993). This change in chemistry was suggested to be the result of slightly accelerated physiological ageing at higher CO_2 levels, which was consistent with a reported shorter growing period and faster plant maturation under elevated CO_2 under greenhouse conditions (e.g. Silvola and Alholm, 1993). However, in long-term field fumigation, enhanced CO_2 (560 ppm) has been reported to delay autumnal senescence of *P. tremuloides* (Taylor *et al*., 2008). Moreover, dynamic salicylates in *S. myrsinifolia* are found to be more abundant in young leaves and organs, while condensed tannins accumulated over the season or in older plant parts (e.g. Julkunen-Tiitto, 1989). Salicylates, such as salicortin and salicin, are known to be key components in Salicaceae biotic anti-stress systems (e.g. Tahvanainen *et al*., 1985; Rank *et al*., 1998; Veteli *et al*., 2002), and thus raised CO_2 levels may have a real impact in the future on the performance of still actively developing species (Julkunen-Tiitto *et al*., 1993). The resembling closed-top climate chamber experiments with CO_2 enhancement of 720 ppm for clonal individuals of *S. myrsinifolia* (grown over one growing season) showed strong clone-specific responses (Veteli *et al*., 2002; Paajanen *et al*., 2011). Interestingly, CO_2 enhancement induced a doubled level of luteolin 7-glucoside in leaves compared with that of the control (Veteli *et al*., 2002); the compound is suggested to have a special defensive role in a plant's survival (Seigler, 1998).

Similarly, confirmed by the graphical vector analyses, a clear accumulation of condensed tannins after 1-month-long exposure of *B. pendula* seedlings to 700 ppm of CO_2 was found, while the activity of several enzymes (phenylalanine ammonia-lyase, polyphenol oxidase and peroxidase) involved with phenolic defence status in plants was also increased (Lavola *et al*., 2000). Moreover, phenolics, such as flavonols and phenolic acids, decreased in the leaves of *B. pendula* seedlings (Lavola *et al*., 1998, 2000) under elevated CO_2. Kuokkanen *et al*. (2001, 2003) conducted close-top climate chamber experiments with CO_2 enhancement of 720 ppm and showed considerable variation in leaf low molecular weight phenolics of *B. pendula* seedlings, while again condensed tannins were markedly increased. Instead, no phenolic changes in the basal or top parts of the stems of *B. pendula* were found, while a number of triterpenoic resin glands increased in the top parts of stems (Mattson *et al*., 2004). Manual defoliation of *B. pendula* seedlings under doubled CO_2 treatment in closed-top chambers only slightly changed chemical defences, as seen in the decrease of total methanol-soluble phenolics (Huttunen *et al*., 2008). Peltonen *et al*. (2005) conducted open-top chamber experiments with two clones (differing their ozone sensitivity) of *B. pendula* saplings (7 years old, soil grown) over 3 years and analysed the chemistry from short-shoot leaves. They found that a doubling of the CO_2 level resulted in about a 19% increased content in leaf condensed tannins, while phenolic acids (+25%), myricetin-glycosides (+18%) and catechin derivatives (+13%) were also increased in this case (Peltonen *et al*., 2005). Moreover, CO_2 responses were seen as even higher levels of two flavonoids (acacetin and pectolinarigenin) in the surface exudates of dormant buds (Peltonen *et al*., 2006). Due to the chamber material used, part of the UV radiation was excluded, and was seen as a 4–37% reduction in several leaf phenolics, including flavone aglycones and flavonol glycosides (Peltonen *et al*., 2005). Lavola *et al*. (2014) conducted closed-top chamber experiments with seed origin seedlings of *B. pendula*, with a doubling of CO_2 and ambient UVB radiation. Doubling of CO_2 concentration markedly increased the concentration of condensed tannins and flavonol myricetins only, covering only six compounds out of 32 identified in the mature leaves of *B. pendula*. It was concluded, based on *B. pendula* young seedling results, that CO_2 could be seen as an intra-plant regulator of carbon allocation between different metabolites (Lavola *et al*., 2000, 2014), and that the variability of the response of *B. pendula* genotypes to elevated CO_2 was much less compared to that of *Salix* genotypes (Lavola *et al*., 2014).

Agrell *et al*. (2001) exposed 1-year-old seedlings of *P. tremuloides* and 2-year-old seedlings of *Betula papyrifera* and *Acer saccharum* to CO_2 (696 ppm) in a greenhouse under two light levels over 2 months. They found a positive effect of CO_2 and light on salicylates (salicortin and tremulacin) in *P. tremuloides* leaves and on tannins in *B. papyrifera* and *A. saccharum* leaves. Interestingly, light availability increased strongly condensed tannins in *P. tremuloides* leaves (Agrell *et al*., 2001). The results of this greenhouse experiment are consistent with the long-term field experiment with *P. tremuloides*, where about 15% and 32% higher levels of salicortin and tremulacin, respectively, were detected under CO_2 concentration of 560 ppm compared with the ambient level (Lindroth *et al*., 2002). However, the authors reported variable and genotype-dependent responses to enhanced CO_2 in tannins in the leaves of *P. tremuloides* trees.

These variable effects induced by enhanced CO_2 on defensive chemistry recall the importance of the interactive effect of other abiotic factors, such as light quality, in such plant phytochemistry studies, because, as shown below for instance, UV irradiation will have a marked effect on the induction of certain plant compounds (Table 4.1). Moreover, controversial results for phenolics and terpenoids in boreal woody species indicate different/higher sensitivity of the shikimic acid–phenylpropanoid pathway leading to phenolics compared with that of the mevalonate pathway leading to terpenoids under enhanced CO_2 concentrations. This may have long-lasting effects on species development and ecosystems relationships (e.g. Peñuelas *et al*., 1997).

4.3 The Effect of Temperature on Defence

Concomitant with atmospheric carbon dioxide increase, several other environmental drivers such as temperature have changed (IPCC, 2007). Generally, enhanced temperature affects plant physiological processes, growth increment, reproduction and survival (e.g. Jamieson *et al*., 2012). Warming climate induces changes in the molecular compositions of individual plants, as have been revealed by gene expression analyses, concomitant changes in the synthesis of different metabolites (e.g. Sardans *et al*., 2011; Peñuelas *et al*., 2013), or in the case of volatiles, released from storage (Loreto and Schnitzler, 2010, and references therein). According to the meta-analysis by Zvereva and Kozlov (2006), including 18 woody species, a general trend was reported for the responses of enhanced temperature; phenolics decreased and terpenes increased in both green plant parts and woody tissues. However, again, studies on the effect of elevated temperature on plants are dependent on many plant-based factors, such as ontogeny, phenology, individual compounds and experimental design, and thus many controversial results for boreal species are also reported. For example, Kuokkanen *et al*. (2001, 2003) found a decrease in some cinnamic acids, flavonol glycosides and (+)-catechin, and an increase in salidoside by temperature enhancement (modulated by ±2°C to ambient levels) in leaves of *B. pendula* seedlings in closed-top chambers. Although defoliation alone decreased the total soluble phenolics in a similar closed-top experiment, the temperature enhancement did not change the phenolic chemistry in the leaves of *B. pendula* seedlings, and it was concluded that even severe foliage wounding (50% defoliation) during the middle or later growing season did not change the

Table 4.1. Effect of UVB, CO_2 and Temperature on the concentrations of salicylates (Sal), phenolic acids (PhAc), flavonoids (Flav), total low molecular phenolics (TLP), stilbenes (Stil), condensed tannins (CT), terpenoids (Terp) and alkaloids (Alk) of some woody boreal species. Upward or downward arrows indicate a significant increase or a decrease in response to the treatment. If nothing else is noted, the results are from leaves.

	Environmental factor				Compound group								
Species	UVB	CO_2	T	In/out	Sal	PhAc	Flav	TLP	CT	Terp	Stil	Alk	Source
A. incana	↓			O			↓						Kotilainen *et al.*, 2008
B. pendula	↑	↑		I		↑	↑			↑			Lavola *et al.*, 2000
B. pendula	↑			O		↑ or 0	↑		0				Tegelberg *et al.*, 2001
B. pendula (bark)	↑			O		↑	↑		0	0			Tegelberg *et al.*, 2002
B. pendula	↓			O		↑	↑		↑				Kotilainen *et al.*, 2009
B. pendula	↓			O		0	↑ or 0		0				Morales *et al.*, 2010
B. pendula	↑	↑	↑	CTC		↑UVB ↓T	↑CO_2 ↑UVB ↓T		↑CO_2				Lavola *et al.*, 2013
B. pendula	↑	↑		I		↓CO_2	↓CO_2 ↑UVB						Lavola *et al.*, 1998
B. pendula		↑	↑	OTC					↑CO_2				Kuokkanen *et al.*, 2001, 2003
B. pendula	↓	↑	↑	OTC		↑CO_2	↑CO_2	↑CO_2					Peltonen *et al.*, 2005
B. pendula		↑	↑	CTC		↑CO_2 ↓T	↑CO_2 ↓T		↑CO_2 ↓T				Veteli *et al.*, 2007

B. pubescens		↑	↑	CTC		↑CO_2 ↓T	↑CO_2 ↓T		↑CO_2				Veteli *et al*., 2007
B. pubescens	↓			O			↑			0			Kotilainen *et al*., 2008
B. pubescens	↑			I		0	↑						Anttila *et al*., 2010
C. vulgaris		↑	↑	O					↑CO_2				Scherber *et al*., 2013
P. abies	↑			O	↑					0			Blande *et al*., 2009
P. abies	↑			O			0			0	0		Turtola *et al*., 2006
P. abies (needles)	↑		↑	O		0	0	0	0		0	↑T	Virjamo *et al*., 2014
P. abies (bark)	↑		↑	O		0	↓T	0	↑UVB		0	↑T	Virjamo *et al*., 2014
P. abies (needles)		↑	↑	I				↓CO_2		↑T ↓CO_2			Sallas *et al*., 2003
P. sylvestris	↑			O			0			0			Turtola *et al*., 2006
P. sylvestris		↑	↑	CTC				0	↑CO_2	↓CO_2			Räisänen *et al*., 2008a,b
P. sylvestris (needles)		↑	↑	I				0		↓CO_2 ↑T			Sallas *et al*., 2003
P. trichocarpa	↑			I	↑/↓		↑						Warren *et al*., 2003
Populus tremula × *Populus tremuloides*			↑	I				↓T					Kosonen *et al*., 2012
S. myrsinifolia		↑		I	↓				↑				Julkunen-Tiitto *et al*., 1993
S. myrsinifolia		↑	↑	CTC	↓T	↓T	↑CO_2 ↓T						Veteli *et al*., 2002

continued

Table 4.1. *continued.*

	Environmental factor				Compound group								
Species	UVB	CO_2	T	In/out	Sal	PhAc	Flav	TLP	CT	Terp	Stil	Alk	Source
S. myrsinifolia	↑			I	0	↑	↑						Turtola *et al.*, 2005
S. myrsinites× myrsinifolia	↑			I	0	↑	↑						Turtola *et al.*, 2005
S. phylicifolia	↑			O		↑	↑		0				Tegelberg *et al.*, 2003
S. myrsinifolia	↑			O	0		↑		0				Tegelberg *et al.*, 2003
S. myrsinifolia	↑		↑	O		↓T	↑UVB ↓T	↓T	↓T				Nybakken *et al.*, 2012 (1 year)
S. myrsinifolia	↑		↑	O	↓T	↓T	↓T		↓T				Nybakken *et al.*, 2012 (2 year)
S. myrsinifolia	↑		↑	O	0/↑ UVB	↓UVB 0/↑T	0/↑UVB ↓T		0				Randriamanana *et al.*, unpublished (3 year)
S. myrsinifolia	↑	↑	↑	CTC	↑CO_2 ↓T	↑CO_2 ↓T	↑CO_2	↑CO_2 ↓T					Paajanen *et al.*, 2011
S. myrsinifolia		↑	↑	CTC	↑CO_2 ↓T	↑CO_2 ↓T	↑CO_2 ↓T		↑CO_2				Veteli *et al.*, 2007
S. myrsinifolia		↑	↑	I	↓T								Nybakken and Julkunen-Tiitto, 2013
S. myrsinifolia (twigs)		↑	↑	I	↓T	↓T	↓T	↑CO_2 ↓T					Nybakken and Julkunen-Tiitto, 2013

Notes: Outdoor experiments = O; Indoor experiments = I; Open Top Chambers = OTC; Closed Top Chambers = CTC.

phenolic defences of *B. pendula* seedlings much (Huttunen *et al*., 2008). Moreover, a closed-top temperature enhancement study with six seed-origin genotypes of *B. pendula* revealed relatively large similarities in their chemical responses, and showed reduced concentrations of several individual quercetin flavonoids in mature leaves, containing about 15% less quercetins than those of ambient-grown seedlings (Lavola *et al*., 2014).

From studies in closed-top chambers, Veteli *et al*. (2002) reported a decrease in total phenolics, and especially in chlorogenic acid, salicylate salicortin and eriodictyol-diglucoside, in the leaves of *S. myrsinifolia* clones. More recently, Paajanen *et al*. (2011) conducted a temperature enhancement experiment in closed-top chambers and also showed a decrease in total phenolics in the leaves of *S. myrsinifolia*. The most responsive compounds in *S. myrsinifolia* leaves were again salicylates and phenolic acids, while the response of flavonoids was significantly clone dependent (Paajanen *et al*., 2011). Responses to temperature enhancements of the dioecious *S. myrsinifolia* (about 2.5–3°C ambient tracking enhancement) have been studied in an experimental field (Nybakken *et al*., 2012) and under greenhouse conditions (Nybakken and Julkunen-Tiitto, 2013). Although nearly all of the 29 leaf compounds detected in the plants from the field experiment were reduced, there were only some gender-specific changes found in the chemistry; aschlorogenic acids were reduced in females and some luteolins were reduced in males (Nybakken *et al*., 2012). In the greenhouse, there were fewer temperature responses in leaf chemistry. Moreover, the temperature stimulation did not affect gender differences in twigs, but three chlorogenic acids were reduced in the leaves of males but not in females (Nybakken and Julkunen-Tiitto, 2013). Another Salicaceae species, the hybrid *Populus tremula* × *P. tremuloides*, grown in greenhouses and exposed to a 2°C temperature elevation, showed consistent and strong decrease of all main phenolics (Kosonen *et al*., 2012). The authors concluded that the decrease of phenolics was due mainly to the dilution by deposition of other compounds, such as cell wall material (Kosonen *et al*., 2012).

Sallas *et al*. (2003) conducted a chamber experiment with 1-year-old *P. sylvestris* and 2-year-old *P. abies* using a day/night temperature of 19/12°C and 23/16°C for controls and elevated temperature chambers, respectively. The concentration of total phenolics in the needles of both species showed no significant change in response to elevated temperature, while there was an increase in total terpenoids that was concluded simply to be associated with thermotolerance of photosynthesis (Sallas *et al*., 2003). Moreover, monoterpenes in *P. abies* stems were more responsive to elevated temperature compared with those of *P. sylvestris*, while an even bigger difference was found for resin acids in both needles and stems (Sallas *et al*., 2003).

The current and 1-year-old needles of 20-year-old *P. sylvestris* trees, grown over 5 years in closed-top chambers, showed no elevated temperature response in phenolics, but in contrast to the results of Sallas *et al.* (2003), there was not much response in the nine monoterpenes identified, maybe due partly to high monoterpene variation between trees (Räisänen *et al*., 2008a).

As to plant-emitted volatiles (including monoterpenes), elevated temperature will increase emission rates exponentially, at least in the short term and measured for *P. abies*, including monoterpenes (Filella *et al*., 2007), and there will be a temperature maximum due to enzyme degradation (Guenther *et al*., 1993). Moreover, it has been estimated that a rise of 2–3°C would increase global volatile emissions by 30–40% (Peñuelas and Llusia, 2003). In boreal areas, accompanied by lengthened growing seasons and warmer winters, this would mean further increased emissions (Peñuelas and Staudt, 2010). For instance, coniferous trees such as *P. sylvestris* and *P. abies* are known to have large stores of volatiles, such as monoterpenes, and are regarded to be moderate emitters (e.g. Räisänen *et al*., 2008a; Ghirardo *et al*., 2010). However, Räisänen *et al.* (2008b) did not detect any temperature effect on monoterpenes in the needles of old *P. sylvestris* individuals grown in top-close chambers having about 2°C ambient tracking temperature elevations.

Temperature seems to be an important factor affecting the alkaloid yield of conifers. For both *Pinus ponderosa* and *P. abies*, concentrations of total piperidine alkaloids in provenance experiments are correlated with the temperature range at which the parental trees have been adapted (Gerson *et al*., 2009; Virjamo and Julkunen-Tiitto, unpublished results). A two-degree increase in temperature in the ambient temperature-tracking field over a growing season resulted in a significant increase in needle alkaloid concentrations of *P. abies* compared to those of the control seedlings (Virjamo *et al*., 2014).

4.4 UVB Effects on Plant Growth and Secondary Metabolites

Highly energetic UVB radiation plays important roles in terrestrial ecosystems. There is a growing body of evidence that UVB radiation of a longer wavelength and/or a low dose plays a regulatory role in plants and induces changes that might extend to other organisms that are interacting with plants, and subsequently changes in ecosystem processes. At low doses of UVB, plants elicit an array of acclimation responses, including morphological changes, accumulation of UVB-absorbing compounds, stimulation of processes for DNA repair, increased production of antioxidant enzymes, etc.

The reducing effect of UVB on plant growth is generally small and less pronounced in woody perennials than in herbaceous plants (Caldwell *et al*., 2007; Li *et al*., 2010). A meta-analysis showed that UVB exposure reduced aboveground biomass by 14.7% and plant height by 10% for plants in polar regions (Newsham and Robinson, 2009). Exceptions, however, exist, since the effect of UVB on plant growth might also vary on the chosen methodologies. Additionally, susceptibility to UVB is species, gender and even genotype specific (Julkunen-Tiitto *et al*., 2005; Robson and Aphalo, 2012). Near-ambient UVB reduced growth parameters such as height, diameter and biomass in field experiments dealing with *Populus deltoides* (Bassman and Robberecht, 2001). UVB also reduced stem and leaf biomass in *Salix phylicifolia*, but that was not the case in *S. myrsinifolia* (Tegelberg *et al*., 2003), *Quercus rubra* (Bassman and Robberecht, 2006), or in *Vaccinium uliginosum* (Boesgaard *et al*., 2012). In most studies with *B. pendula*, UV treatment had no effect on plant height and biomass (Tegelberg *et al*., 2001; Kotilainen *et al*., 2009; Morales *et al*., 2010; Lavola *et al*., 2014). In *P. abies*, UVB did not affect needle, branch or plant biomass production, but only branch diameter (Sedej and Gaberščik, 2008).

Most studies in both herbaceous and woody species indicate that the effects of insect herbivory on plants would be determined by changes in the host plant tissues, which is in turn affected by UVB (Caldwell *et al*., 1998). The increase in the concentration of secondary metabolites that absorb UVB was the most typical and consistent response to UVB, and in general, UVB exposure increases the concentration of such compounds by 7.4% in Arctic plants (Newsham and Robinson, 2009) and by 10% in most vascular plants (Searles *et al*., 2001). Phenolic compounds occur universally in plants, and the production of phenolic compounds such as flavonoids and phenolic acids (mainly hydroxycinnamic acids and their esters), are among the most characterized acclimation response of plants in response to UVB (Julkunen-Tiitto *et al*., 2005). A comparative and interactive study of three factors – UVB, CO_2 and temperature – on silver birch indicated that UVB was the most effective environmental factor to induce flavonoid synthesis (Lavola *et al*., 2014). Supplemental UVB also increased the concentration of UVB-absorbing compounds in different deciduous species such as *Populus trichocarpa* (Warren *et al*., 2002). Apart from their role in screening UVB light, flavonoids are also suggested to be efficient reactive oxygen species (ROS) scavengers, due to their distribution in the chloroplast, vacuoles and nucleus, which are near or within the sites of ROS production (Agati and

Tattini, 2010; Agati *et al*., 2012, 2013). A certain group of flavonoids, flavonols (such as quercetin and luteolin glycosides), would have greater antioxidant properties than luteolins and apigenins, due to their orthodihydroxy B-ring substitution (Agati and Tattini, 2010).

Even among woody species, the degree of tolerance to UVB differs (Table 4.1). In most deciduous trees and shrubs, the accumulation of quercetins, quercetin derivatives and phenolic acids is often reported. A solar-tracking field experiment showed that UVB induced an increase in the concentrations of quercetins in the leaves of different clones of *S. myrsinifolia* (Tegelberg *et al*., 2003). In *S. phylicifolia* leaves, UVB also increased the total amount of phenolic acids (Tegelberg *et al*., 2003). A more recent solar-tracking field experiment over 2 years with *S. myrsinifolia* also reported that enhanced UVB (estimated at a 20% O_3 decrease) increased the concentrations of quercetin 3-galactoside (hyperin) and some other quercetin glycosides (Nybakken *et al*., 2012). In *B. pendula*, the accumulation of quercetins and quercetin derivatives has often been reported under enhanced UVB (Tegelberg *et al*., 2001; Lavola *et al*., 2014). The concentration of a phenolic glucoside, 3,4′-dihydroxypropiophenone-3-glucoside (DHPPG), was also increased by UVB in the bark of *B. pendula* (Tegelberg *et al*., 2002). In a UV-exclusion experiment, apart from quercetins, concentrations of condensed tannins, chlorogenic acid and the concentration of other flavonoids such as myricetins and kaempferols in the leaves of *B. pendula* were also increased by the ambient UVB level (Kotilainen *et al*., 2009). In *Betula pubescens*, UVB induced the accumulation of myricetin glycosides in a greenhouse experiment (Anttila *et al*., 2010). In *Alnus incana* leaves, the main secondary metabolites such as stilbenes and condensed tannins were not affected by UV exclusion (Kotilainen *et al*., 2008). Warren *et al*. (2003) reported that in a greenhouse experiment, a double increase in UVB increased leaf salicortin significantly for *P. trichocarpa*. Even though most salicylates absorb less UVB radiation than flavonoids at similar concentrations, salicylates such as salicortin and tremulacin might still act as UVB-absorbing compounds, as they absorb strongly in the UVB region, especially in the shorter wavelengths (Warren *et al*., 2003).

Coniferous species with thick needle structure are thought to be tolerant to UVB radiation. Both constant levels of highly UVB-absorbing phenolics (Strack *et al*., 1989; Turunen *et al*., 1999; Rummukainen *et al*., 2007) (Fig. 4.1), as well as structural properties such as epidermal thickness and cuticle, are protecting mesophyll from harmful radiation (Laakso and Huttunen, 1998). While UVB was also reported to enhance the concentrations of flavonoids such as kaempferol and quercetin 3-glucoside in the epidermal cells of the needles of *P. sylvestris* (Harborne and Williams, 2000), UVB-treated conifers often show no consistent increase in secondary metabolites. Such invariability in UV-absorbing compounds in conifers argues that they are more resistant to UVB than other woody perennials. However, the long lifespan of the needles has raised questions about the cumulative effects of long-lasting exposure to increased UVB radiation. In a 5-year field experiment with *P. abies*, the concentrations of phenolics were not affected by enhanced UVB (Sedej and Gaberščik, 2008). Similarly 2- and 3-year outdoor experiments with *P. abies* and *P. sylvestris*, respectively, resulted in no significant changes in phenolics or terpenes (Turtola *et al*., 2006). Neither did UVB appear to affect the volatile organic compound (mono- and sesquiterpenes) emissions of needles of *P. abies* shoots (Blande *et al*., 2009). Most studies have focused on needle chemistry, but recently bark has been shown to increase significantly concentrations of condensed tannins as a response to elevated UVB radiation in *P. abies* seedlings (Virjamo *et al*., 2014). Moreover, in a solar-tracking field experiment, concentrations of piperidine alkaloids in the needles of *P. abies* have been shown to be unaffected by increased UVB radiation (Virjamo *et al*., 2014). In conclusion, most studies have shown that most trees and shrubs develop resistance to realistic UVB enhancement by gradually accumulating flavonoids (quercetins and kaempferols) and phenolic acids. The UVB effects on woody perennials, however, cannot be generalized, and other environmental factors such as plant development stage, phenology and the plant's nutritional status and other factors should be taken into account as they might also influence plant susceptibility to UVB.

4.5 Combining Manipulations – Increasing Effects or Effect Dampening?

Although most experiments testing climate change effects on woody plants have dealt with changes in one environmental factor, the phenomenon is indeed more complex than that in nature (Table 4.1). Most places in the world will, in the future, face changes in two or more climatic factors simultaneously (IPCC, 2007, 2013), and scientists are only beginning to understand how the interaction of these factors may impact on plants. Complexity and costs limit how representative, comprehensive and long-lasting multifactor experiments may be. Most such studies have, to date, been conducted in advanced growth chambers or greenhouses, but a few outdoor facilities are emerging. In Joensuu (Eastern Finland), a field for modulated enhancements of UVA, UVB and temperature (T) was set up in 2009. So far, it has hosted a 3-year study of *S. myrsinifolia* and two growing seasons of *Populus tremula*. Some of the FACE (free-air CO_2 enhancement) experiments have also been evolved to include manipulations of other climatic factors (e.g. Huxman *et al*., 1998; Kimball *et al*., 2001). The Danish CLIMAITE experiment (Mikkelsen *et al*., 2008) simultaneously changes CO_2, T and precipitation over a dry heath/grassland landscape, and the experiments combining CO_2 and UVB at the Abisko Scientific Research Station in Swedish Lapland also include some woody plants. But so far, little has been published on the effects on plant secondary chemistry from these experimental settings.

Combinations of two or more climatic changes that influence a defensive compound in the same direction may cause an additive effect when they are combined, i.e. the effect size is the sum of what results from the single-factor treatments. One could also imagine that synergistic effects are possible, i.e. that the combined effect is bigger than the sum of the single factors. Climatic factors may also have antagonistic effects, which means that they work in opposite directions and possibly cancel each other out, or at least reduce the combined effect in comparison to the single factors.

CO_2 and temperature are maybe the two most-studied single factors of climate change, and there are also quite a few combination studies available. In a meta-analysis from Zvereva and Kozlov (2006), it was found that the opposite effects of elevated CO_2 (increase) and temperature (T) (decrease) on phenolics in general cancelled each other out in combination. Terpenes, on the other hand, which did not respond to elevated CO_2 alone, increased under both elevated T and the combination treatment. The degree of responses of defensive secondary compounds to treatments differed between woody and green tissues, as well as between gymnosperm and angiosperm plants. In later studies, this general picture of the combined effect was confirmed in *B. pendula*, *B. pubescens* and *S. myrsinifolia* by Veteli *et al*. (2007), and in *S. myrsinifolia* by Nybakken and Julkunen-Tiitto (2013).

The combination of UVB and CO_2 has not been much studied on woody species. In an experiment with *B. pendula* (Lavola *et al*., 2000), the typical UVB induction of flavonoids was reduced under high CO_2 concentrations, while other groups of compounds increased under the combined treatment. This was explained by increased access to CO_2 causing changes in metabolic activities that overruled the ones caused by UVB.

Quite a few studies have combined manipulations of CO_2 and water availability, but few of these are from the boreal zone, and none of the existing studies seem to have measured chemical defence (same conclusion as a review by Robinson *et al*., 2012). In the above-mentioned CLIMAITE experiment, Scherber *et al*. (2013) studied insect herbivore performance under enhancements of CO_2, drought and T. Leaf tannin content increased under elevated CO_2, but there did not seem to be effects from the other treatments or treatment combinations. Other phenolic compounds were not measured.

Drought in combination with UVB has also been tested mostly in temperate or tropical climates and/or with crop plants, but Turtola *et al*. (2005) tested the effect of drought stress in combination with UVB on the hybrid *Salix myrsinites* × *S. myrsinifolia* and on *S. myrsinifolia* in a 4-week greenhouse experiment. In drought-stressed plants, a UVB-induced accumulation of phenolic acids was reduced, while the flavonoid accumulation was the same as in well-watered plants. Moreover, in the above-mentioned 3-year experiment with field-grown *S. myrsinifolia* under combined enhancements of UVB and T, there were few interactive effects of the treatments (Nybakken *et al*., 2012; Randriamanana *et al*., unpublished results). Only some salicylates seemed to be facilitated under the combined treatment (UVB + T) in comparison with single-factor treatments in the first year. Apart from this, only the usual single-factor effects were found; decreased concentrations under elevated T and some increases in quercetins under elevated UVB. It is, however, worth mentioning that the decreasing effect of T on phenolic concentration diminished over the experimental time, with the highest effect in the first year and no effect in the last year.

In closed-top chambers with enhancements of UVB, CO_2 and T, Lavola *et al*. (2014) found that condensed tannins, most flavonols and phenolic acids in *B. pendula* accumulated under elevated CO_2 and UVB, while the effect disappeared under the triple treatment. Paajanen *et al*. (2011) studied *S. myrsinifolia* from the same experimental setup. Athough total phenolics increased at elevated CO_2 and decreased at elevated T, there was no interactive effect found in combined CO_2, temperature and UVB. In this study, the clone decided if the plants under the triple treatment behaved as under temperature or CO_2 only.

From the few multifactor studies of northern woody species so far, we may conclude that there is nothing that points towards amplification of effects when two or more climatic factors are changed simultaneously. The general picture seems to be that the combined treatments give effects lower or equal to single treatments. Leuzinger *et al*. (2011) speculate that increasing scale and treatment complexity in general might lead to size dampening, which might mean that the predicted impact of global change would be reduced compared to what has been proposed based on small-scale and single-factor experiments. However, although the secondary chemistry of plants has been a popular research subject for decades, there is clearly a need for more research, especially long-term studies on boreal woody plants in relation to climate change. With the future projections for the area in mind (e.g. IPCC, 2007), studies combining manipulations of temperature and precipitation could be identified as being especially urgent for the years to come.

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5

Effects of Climate Change on the Interactions Between Insect Pests and Their Natural Enemies

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Abstract

All biological rates depend on temperature, as they are based on biochemical reactions. Hence, the same holds for feeding rates and their functional components. From a 'biologically relevant' scope, feeding rates increase exponentially with temperature. Recent studies suggest that this increase of feeding rates with warming is shallower than the increase in metabolism. Theoretically, this mismatch should lead to a lower numerical response of biological control agents, presumably resulting in a higher probability of insect pest outbreaks. While depending on temperature, the more complex, non-linear nature of feeding rates further implies that they are also critically dependent on prey densities (i.e. the functional response). The fundamental elements of the functional response are the capture rate and the handling time. Basically, the capture rate determines the feeding success at low densities, whereas the handling time determines the maximum amount a predator is able to consume in a given time window. Moreover, capture rates themselves can also depend on prey density, turning a hyperbolic type II into a sigmoid type III functional response. This shift in the shape of the response is introduced by refuges for the prey, among other mechanisms. Contrasting the type II functional response, type III functional responses are well known to promote stable population dynamics and community structure. Therefore, changes in habitat complexity driven by climate change might also affect feeding interactions and insect pest control. Here, we review how climate change influences the functional responses of predator–prey and parasitoid–host pairs directly via increased temperature and indirectly via changes in habitat structure. We complement our review by exploring the potential consequences of feeding relations that are altered by climate change-induced mechanisms, through the application of model simulations of such consumer–resource population dynamics.

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5.1 General Introduction

Climate change is an umbrella term of various effects, including increasing global temperature, changes in temperature variability, precipitation, increasing CO_2 and a higher frequency of extreme weather events. Global warming accelerated throughout the last century, as indicated by an annual increase of 0.07°C from 1906 to 2005 compared to an increase of 0.13°C from 1956 to 2005 (IPCC AR4 – Trenberth and Josey, 2007). Projections of an increase in global surface temperature in 2100 range from 1.8°C to 4°C (IPCC AR4 – Meehl *et al*., 2007). It seems inevitable that these changes will have a strong impact on the distribution and performance of the biosphere, and a vast majority of the species within. Therefore, climate change and global warming have recently been among the 'hottest' topics in the ecological and environmental sciences (e.g. Petchey *et al*., 1999; Walther *et al*., 2002; Parmesan and Yohe, 2003; Deutsch *et al*., 2008; Tylianakis *et al*., 2008; Loarie *et al*., 2009; Brose *et al*., 2012). In this realm of research, one focus is set on documenting the altered geographical distributions of species and biomes (e.g. Lawler *et al*., 2009; Loarie *et al*., 2009), while the phenological shifting of species activities is covered elsewhere (e.g. Parmesan, 2007). Additionally, there is research addressing the underlying physiological processes by examining the thermal tolerance windows of particular species and matching it with climate change predictions (Deutsch *et al*., 2008). While these approaches concentrate mainly on autecological questions and the underlying mechanisms, there have been repeated calls to look particularly at higher levels of ecological organization and investigate the effects of climate change on trophic and non-trophic species interactions (Kareiva *et al*., 1993; Walther *et al*., 2002; Schmitz *et al*., 2003; Tylianakis *et al*., 2008). In this vein, warming and climate change effects on pairwise species interactions (e.g. predator–prey or parasitoid–host), as well as more complex community-level interactions (e.g. food webs), have been examined, particularly with experimental approaches in laboratory environments, with the consistent finding that higher-order consumers (e.g. predators) are most prone to extinction compared to producers (e.g. plants) and primary consumers (e.g. herbivores) (e.g. Petchey *et al*., 1999; Rall *et al*., 2010; Vucic-Pestic *et al*., 2011; Fussmann *et al*., 2014). Experimental approaches that heat terrestrial field mesocosms are relatively rare and have provided no straightforward results so far (e.g. Barton *et al*., 2009), whereas structural alterations on the community level have been examined from field data (Voigt *et al*., 2003). As in the microcosm studies, those studies suggest that the highest trophic levels are most sensitive to environmental changes (see also Berggren *et al*., 2009).

One important secondary effect of climate change might be habitat loss, due not only to an increase in the numbers of extreme weather events (e.g. loss of habitat-providing plants) but also to sea level rise, not forgetting directly human-driven alterations and degradation of primary natural habitats (often subsumed under the term 'land-use change'). The structural complexity of habitats is well known to affect not only species distribution and abundances but also interaction patterns – which has been well documented, particularly early on for aquatic systems (e.g. Heck and Thoman, 1981; Diehl, 1988) and also later for terrestrial systems (e.g. Finke and Denno, 2002; Langellotto and Denno, 2004). Besides those findings from rather basic research-oriented work, there is the urgent need to integrate these conceptual approaches with merely applied perspectives. For instance, climate-induced changes will impose severe impacts on human agricultural systems by affecting crop yields both directly and indirectly (Fuhrer, 2003). Hence, biological control agents of insect pests might also be affected significantly, as reviewed by Thomson *et al*. (2010) and Hance *et al*. (2007). The bulk of research represented in those reviews had focused particularly on phenological issues where climate change had often caused or facilitated unfavourable spatio-temporal disruptions of predator–prey interactions. However, this approach of characterizing temperature effects on species interactions has certain shortcomings, particularly if we are to develop a framework to improve the forecasting capabilities in ecology. The idiosyncratic nature of spatio-temporal synchronization or disruption patterns that are related to the ranges and edges of species distributions still impede the development of a mechanistic framework to provide rational null models with global applicability (Sexton *et al*., 2009). In contrast, models that are based on fundamental biological rates such as growth, feeding and death should be considered as a reasonable alternative. Such models can be simple consumer–resource models (Rosenzweig and MacArthur, 1963; Yodzis and Innes, 1992) or may scale up to whole-community models (Brose *et al*., 2006b; Rall *et al*., 2008), and have been used to predict experiments from microcosms to whole ecosystems (Boit *et al*., 2012; Schneider *et al*., 2012). The temperature dependence of the rates needed to parameterize such models has already been thoroughly investigated (Brown *et al*., 2004; Savage *et al*., 2004; Dell *et al*., 2011; Ehnes *et al*., 2011; Englund *et al*., 2011; Rall *et al*., 2012; Fussmann *et al*., 2014). In the remainder of this chapter, we will set our focus on the presumably most important of these rates, the feeding rate, and how the strength of feeding interactions depends on temperature (Brown *et al*., 2004; Englund *et al*., 2011; Rall *et al*., 2012) and structural habitat complexity (Vucic-Pestic *et al*., 2010a; Kalinkat *et al*., 2013a) and what this means for the specific interactions between insect pests and their natural enemies.

5.2 A Conceptual Definition of Trophic Interactions

The idea of density-dependent feeding rates has a long tradition in animal ecology. While the first formulation of this concept was introduced by Solomon (1949), the majority of credits for its introduction are usually given to Holling for introducing the methodological and mathematical framework (Holling, 1959a,b). There, the per capita feeding rate, F, is formulated as a function of the instantaneous rate of successful attacks, a (often called attack rate; hereafter, we will use the term capture rate), the handling time, h, and the resource density, N:

$$F = \frac{aN}{1 + ahN} \tag{5.1}$$

with the typical hyperbolic type II response (Fig. 5.1a). This sublinear feeding dependency leads to a decrease in per capita predation risk (Fig. 5.1b). Due to this decreasing predation risk, the type II functional response is known to be reasonable for non-stable population dynamics (Oaten and Murdoch, 1975; Yodzis and Innes, 1992; Rall *et al*., 2008), but we will discuss this in more depth below. Starting from this basic notation, a plethora of different functional response models can be derived (Jeschke *et al*., 2002). The possibly most prominent derivations are the type I functional response (Fig. 5.1c), the type III functional response (Fig. 5.1e) and the generalized functional response (Fig. 5.1g; Williams and Martinez, 2004; Rall *et al*., 2008; Kalinkat *et al*., 2013b). The type I functional response can be derived easily by assuming that the handling time of the predator is negligible, yielding a linear function:

$$F = aN \tag{5.2}$$

This linear increase in feeding leads to a constant per capita predation risk to the prey (Fig. 5.1d). The type I functional response has some conceptional weaknesses, such as the missing satiation of a predator individual. Some authors overcome this problem by describing their empirical results with two linear lines; an increasing linear feeding rate up to a cut-off level, followed by a horizontal maximum feeding rate. (Note that some authors call the version with a cut-off level as type I, and the strictly linear increasing version as type 0 functional response.) The type I functional response, however, was deemed to be an experimental artefact, as researchers chose too small a prey density gradient, often ignoring very low and high prey densities (Sarnelle and Wilson, 2008). The type III functional response is the next more complex variant in the functional

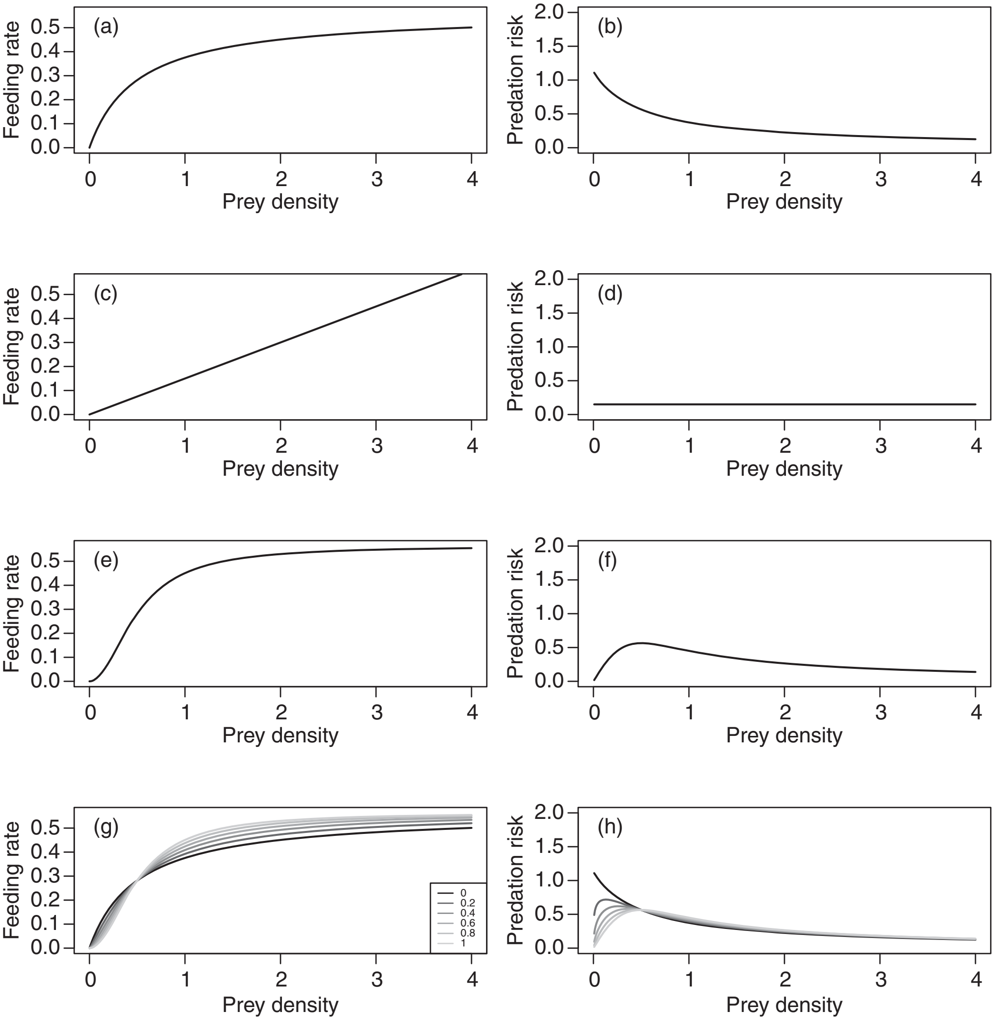

Fig. 5.1. Types of functional responses. The feeding rates as a function of prey density (a,c,e,g) and the predation risks as a function of prey density (b,d,f,h). First row displays the type II functional response (a,b); the second row displays the type I functional response (c,d); the third row displays the type III functional response (e,f); the fourth row displays the generalized functional response (g,h).

response hierarchy (Fig. 5.1e). Here, the capture rate, a, is also prey density dependent. In the simplest form, the capture rate follows a linear relationship with prey density:

$$a = bN \tag{5.3}$$

where b is the capture coefficient. Incorporating this equation into Eqn 5.1 leads to:

$$F = \frac{bN^2}{1 + bhN^2} \tag{5.4}$$

Again, the predation risk takes a different shape (Fig. 5.1f). At the lowest prey densities, increases in prey density lead to a higher predation risk, and to very stable population dynamics (Oaten and Murdoch, 1975; Yodzis and Innes, 1992; Rall *et al*., 2008). Leslie Real (1977, 1979) extended this categorical thinking of ‘types’ of functional responses by suggesting a more flexible notation of the functional response model, allowing a continuous shift of a type II into a type III functional response (Fig. 5.1g). Following well-established models of enzyme kinetics (Barcroft and Hill, 1910), Real (1977) extended Eqn 5.3 by an additional coefficient, which was later termed the Hill exponent, H (Brose *et al.*, 2006b). For mathematical practicability, the Hill exponent was also described as $H = q + 1$ (Williams and Martinez, 2004; Kalinkat *et al.*, 2013b), with q being termed the capture exponent, resulting in the following formulations for the capture rate (Kalinkat *et al.*, 2013b):

$$a = bN^{q} \tag{5.5}$$

and the functional response:

$$F = \frac{bN^{1+q}}{1 + bhN^{1+q}} \tag{5.6}$$

Here, if the capture exponent q is set to zero, the functional response falls back to the original type II functional response, but an increase of q leads to a shift from the hyperbolic curve (type II) to the sigmoid curve (type III). Interestingly, at intermediate values of $q \sim 0.2$, the appearance of the functional response curve looks fairly similar to the above-described type I functional response with a cut-off level. This modification of the functional response also translates into a shift of predation risk from a destabilizing decreasing predation risk to a more stabilizing hump-shaped predation risk (Fig. 5.1h). We will discuss the resulting consequences on the stability of consumer–resource relations in more detail below.

5.3 Methods

5.3.1 Modelling

We used a bioenergetic population dynamics model following Yodzis and Innes (1992) where P presents the density of the predator (or parasitoid):

$$\frac{\Delta N}{\Delta t} = rN\left(1 - \frac{N}{K}\right) - \frac{\omega_F F_{max} N^{1+q}}{N_0^{1+q} + N^{1+q}} P \tag{5.7a}$$

$$\frac{\Delta P}{\Delta t} = \frac{e\omega_F F_{max} N^{1+q}}{N_0^{1+q} + N^{1+q}} P - \omega_m m P \tag{5.7b}$$

where r is the intrinsic growth rate; K is the carrying capacity; F_{max} is the maximum feeding rate defined as the inverse of the handling time; m is the metabolic rate; ω_F and ω_m are the temperature dependencies of the maximum feeding rate and the metabolism, respectively; e is the assimilation efficiency; q is the shaping parameter changing the type of the functional response; and N_0 is the half saturation density that is defined as the inverse of capture rate times handling time (1/a*h). The maximum feeding rate, F_{max}, is calculated by:

$$F_{max} = ym \tag{5.8}$$

where y is the relative maximum feeding rate. The specific metabolic rate (metabolic rate per gram body mass) follows a negative ¼ power law with body mass (Peters, 1983; Yodzis and Innes, 1992; Brown *et al.*, 2004):

$$m = m_0 R^{-0.25} \tag{5.9}$$

where m_0 is a constant that is set to 0.2227 for predator–prey pairs (Otto *et al.*, 2007) and R is the relative body mass to the basal species. If not otherwise stated, the rates are set as follows: $r = 1$; $K = 1$; $y = 8$; $N_0 = 0.5$; $\omega_F = 1$; $\omega_m = 1$; $e = 0.85$; $q = 0$; $R = 100$ (Yodzis and Innes, 1992; McCann and Yodzis, 1994; McCann and Hastings, 1997; McCann *et al.*, 1998; Williams and Martinez, 2004; Brose *et al.*, 2005, 2006a,b; Otto *et al.*, 2007; Rall *et al.*, 2008).

To model the mismatch of warming, we used a generalized version of the Arrhenius equation (Gillooly *et al.*, 2001; Petchey *et al.*, 2010; Rall *et al.*, 2012):

$$\omega_{F,m} = e^{\frac{E\left(T_{Kelvin} - T_0\right)}{kT_{Kelvin}T_0}} \tag{5.10}$$

where E is the activation energy, T_{Kelvin} is the absolute temperature in *Kelvin*, k is the Boltzmann constant and T_0 is the normalization constant defining the position of the intercept of the ln-transformed Arrhenius equation.

All simulations were performed using C++ and using the GNU Scientific Library (GSL) (Version 1.15). We used a Runge–Kutta–Fehlberg fourth-order algorithm (with a fifth-order error estimate) with adaptive step size. The initial step size was 10^{-5}, a relative tolerance of 10^{-12} and an absolute error tolerance of 10^{-14}. The total length of each time series was 200,000 time steps, and we analysed the last 1500 time steps to avoid transient dynamic effects.

5.3.2 Database

We used the database set up by Rall *et al.* (2012). We analysed the temperature dependence on studies investigating ladybeetles that had at least three different temperature treatments (Munyaneza and Obrycki, 1997; Xia *et al.*, 2003; Gotoh *et al.*, 2004; Isikber, 2005; Sentis *et al.*, 2012) and we added data on parasitoids (Cave and Gaylor, 1989; Flinn, 1991; Enkegaard, 1994; Smith, 1994; Flinn and Hagstrum, 2002; Menon *et al.*, 2002; Zamani *et al.*, 2006) ($n = 129$). For the ladybeetles, the final data set contained both juvenile and adult live stages. See Xia *et al.* (2003) for an example of how warming and the life stages of ladybeetles influence functional responses.

To analyse the occurrence of habitat structure, type of functional response and experimental settings, we restricted the data set by Rall *et al.* (2012) to terrestrial invertebrates ($n = 313$).

5.3.3 Statistics

We ln-transformed both the capture rates and the handling times to improve normality and to test for an exponential relationship using linear models. We transformed the temperature in Kelvin to the Arrhenius temperature (see Section 5.4 for the biological background):

$$T_{Arrhenius} = \frac{\left(T_{Kelvin} - T_0\right)}{kT_{Kelvin}T_0} \tag{5.11}$$

where $T_{Arrhenius}$ is the Arrhenius temperature; T_{Kelvin} is the total temperature in Kelvin; k is the Boltzman constant (0.00008617343 eV Kelvin$^{\wedge-1}$); and T_0 is the normalization constant shifting the intercept into the range of the data ($T_0 = 293.15\,Kelvin = 20°C$).

All data analyses were performed in R (R Development Core Team, 2013). We applied mixed-effects models (Pinheiro *et al.*, 2014) with the dependent variables ln-transformed handling time and ln-transformed capture rate, the independent variables Arrhenius temperature, the square transformation of the Arrhenius temperature and the two feeding interaction types, ‘ladybeetle’ and ‘parasitoid’, as well as the interactions between the feeding interaction types with the linear Arrhenius temperature and the squared Arrhenius temperature. We used the study as a random effect that acts on the Arrhenius temperature (slope) and the two different interaction types (intercepts). We used the backward selection method ‘stepAIC’ (package ‘MASS’; Venables and Ripley, 2002) for model selection. To cope with optimization problems, we set the control settings of the lme.function to: maxIter = 500, msMaxIter = 500 and opt = ‘optim’. To use the stepAIC function, we set the method to ‘ML’.

We additionally reanalysed the capture exponent, q, from the study of Vucic-Pestic *et al.* (2010b) with a sigmoid function using the nls function in R, following the more recent analyses of Kalinkat *et al.* (2013b):

$$q = \frac{q_{max}R^2}{R_0^2 + R^2} \tag{5.12}$$

where q_{max} is the satiation of the curve and R_0 denotes the body mass ratio of the predator to the prey where $q_{max}/2$ is reached.

5.4 Warming, Changes in Interaction Strength and Consequences for Stability

5.4.1 Background

Temperature, and therefore warming, influences biological rates on all scales, from basal metabolic demands (Brown *et al.*, 2004; Sibly *et al.*, 2012) up to the highest organizational levels (e.g. community structure; Yvon-Durocher *et al.*, 2011). Generally, the temperature dependence of biological rates is described by the Arrhenius equation (Gillooly *et al.*, 2001; Brown *et al.*, 2004):

$$x = x_0 e^{\frac{-E_x}{kT_{kelvin}}} \tag{5.13}$$

where x is a biological rate; x_0 is a constant; k is the Boltzman constant; T_{Kelvin} is the absolute temperature in Kelvin; and E_x is the activation energy. During the past one and a half decades, this relationship suffered a lot of criticism, including the question of what is the right overall universal activation energy (Clarke, 2004; Clarke and Fraser, 2004) or whether or not an exponential relationship is correct (Knies and Kingsolver, 2010). These discussions, however, are beyond the scope of this study. To date, most empirically documented rates show a hump-shaped relationship with increasing temperature for analyses of intraspecific, individual-based data (Pörtner *et al*., 2006; Pörtner and Farrell, 2008; Knies and Kingsolver, 2010), whereas meta studies looking at interspecific patterns often compare only the increasing part of the hump. This seems to be justified, due to the fact that, in the majority of cases, this represents the biologically relevant temperature scope (Savage *et al*., 2004; Fussmann *et al*., 2014). Alternatively, the data are split into two separatly exponential ranges (Dell *et al*., 2011).

While metabolism is the most prominent biological rate to be addressed in this field of research (Brown *et al*., 2004; Sibly *et al*., 2012), feeding rates are also known to increase with increasing temperature within a biologically relevant range. This has been shown for general terrestrial predators (Rall *et al*., 2010) and also for butterfly larvae such as *Manduca sexta* (Kingsolver and Woods, 1997, 1998). More precisely, the handling time decreases with increasing temperature, whereas the capture rate increases (Vucic-Pestic *et al*., 2011; Sentis *et al*., 2012). These relationships might break down if the temperature range extends the biologically relevant range, where the feeding rates and their components (i.e. capture rates and handling times) might show a hump-shaped behaviour (Kingsolver and Woods, 1997, 1998; Englund *et al*., 2011; Rall *et al*., 2012; Sentis *et al*., 2012). For instance, Englund *et al*. (2011) reported hump-shaped relationships for both handling time and capture rates, while Rall *et al*. (2012) found a hump-shaped relationship just for handling time and not for capture rates. To increase the confusion, case studies (e.g. Sentis *et al*., 2012) found a hump-shaped relationship for capture rates but not for handling times. There is no exact or unique explanation for this yet, but it seems that hump-shaped relationships are smoother in aquatic systems as it is common to use them in the aquatic sciences (Pörtner *et al*., 2006; Pörtner and Farrell, 2008), whereas Sentis and colleagues (2012) carried out feeding experiments close to the upper lethal temperature boundary and did not find hump-shaped relationships.

In general, an increase of feeding rates with warming suggests that biocontrol agents should be more efficient in controlling prey populations due to increased per capita feeding. This might be true on a very short timescale, but the picture might change when also taking into account other biological rates such as metabolism and death. Recent studies suggest that not only the absolute increase in feeding determines the stability of predator–prey systems, but rather the *relative* rates (Yodzis and Innes, 1992; Vasseur and McCann, 2005; Fussmann *et al*., 2014). One of the best documented of such relative rates is the relative interaction strength, which is the ratio of feeding (more precisely, the maximum feeding rate) to the metabolic demands (Yodzis and Innes, 1992; Rall *et al*., 2010; Vucic-Pestic *et al*., 2011; Iles, 2014). Vasseur and McCann (2005) showed that, by using data from a meta study of Hansen *et al*. (1997), the response of maximum feeding rates to warming was more pronounced than the response of metabolic demands (i.e. the feeding rate increased faster than the metabolism). This leads to an increase of relative feeding rates and subsequently to a decrease in stability. More precisely, overall biomass densities decrease with increasing temperature, while the amplitudes of population cycles simultaneously increase (Fig. 5.2a). This effect on population cycles can subsequently lead to extinction of the predator or the prey by stochastic events (Rosenzweig, 1971) or by reaching a lower lethal population boundary (Williams and Martinez, 2004; Brose *et al*., 2008). More recent studies on terrestrial invertebrate predators,

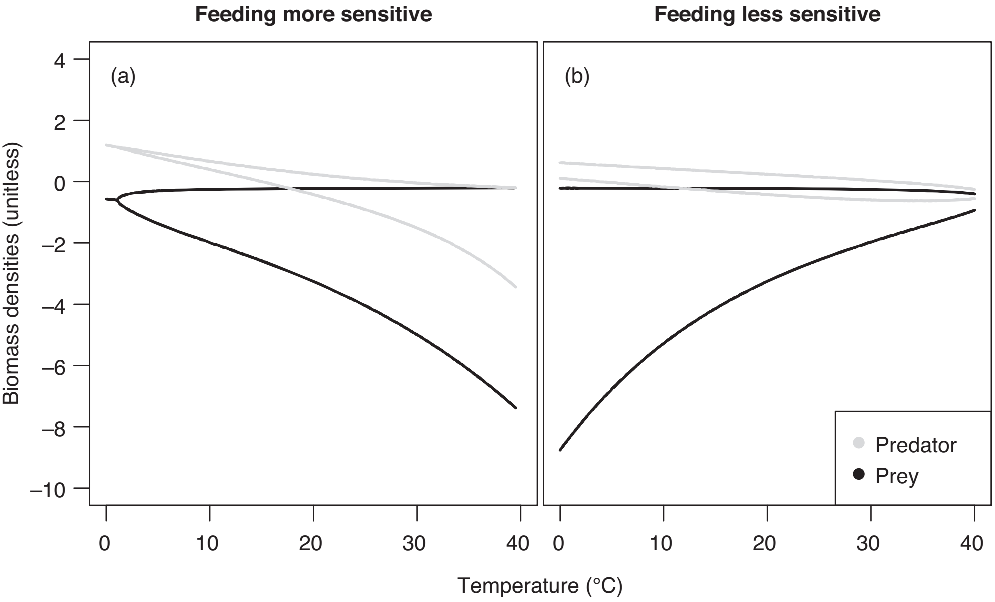

Fig. 5.2. Population responses to warming. A bifurcation diagram showing how population dynamics change due to warming. The points display the minima and maxima of a single time series at a given temperature. The left plot (a) displays the results *sensu* Vasseur and McCann (2005); the right plot (b) displays the results *sensu* Rall and colleagues (Rall *et al*., 2010; Vucic-Pestic *et al*., 2011; Fussmann *et al*., 2014).

however, have shown the opposite scaling. There, the feeding rate is less sensitive to warming compared to the metabolic demands, which leads to a reduced feeding efficiency (Rall *et al*., 2010; Vucic-Pestic *et al*., 2011). Subsequently, population stability is enhanced (Fig. 5.2b). As in the first scenario, overall biomass densities decrease. Hence, it follows that, in extreme cases, the predator may starve to death because it is no longer able to fulfil its metabolic demands (Rall *et al*., 2010; Vucic-Pestic *et al*., 2011; Iles, 2014). Supporting these findings, Fussmann *et al*. (2014) recently reported that in most combinations of empirically documented temperature dependencies of biological rates, simulated predator–prey models showed a stabilizing behaviour, with subsequent extinction of the predator (73.6%).

To address these theoretical population dynamic consequences in a more specific context, and based on empirical data from natural biocontrol agents, we were looking for analyses of feeding-rate relations with warming. Although there were a number of case studies available (see Section 5.3.2), to our knowledge, a respective meta-analysis that focused on how functional–response parameters of biocontrol agents changed due to warming was missing. To address this knowledge gap, we focus here on two biocontrol agent groups, namely parasitoids and ladybeetles. We therefore analysed handling times and capture rates using a polynomial model up to the second order, with the possibility for interactions between the biocontrol agent type and both the linear and the squared temperature term (see Section 5.3 for details). The type of biocontrol agent (ladybeetle/parasitoid) interacts with both the linear and squared temperature term in the handling time model (Table 5.1). Note that the interaction of the linear term is only marginally significant, but according to the Akaike information criterion (AIC), the term is necessary to describe the data. Generally, parasitoids have higher handling times (Fig. 5.3a). Moreover, the handling times for parasitoids have a steeper increase with

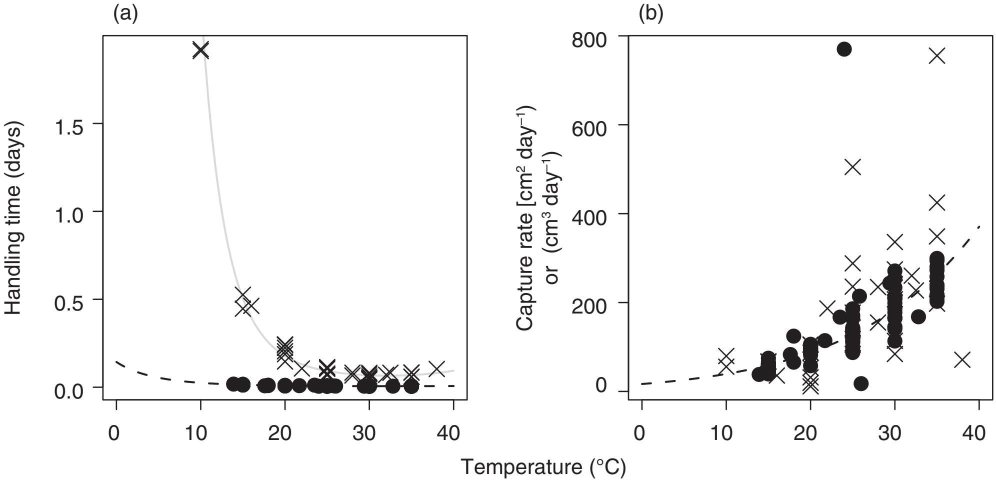

Fig. 5.3. Temperature dependence of functional response parameters. Handling times (a) show an inverse hump-shaped relationship and capture rates increase with the exponential Arrhenius relationship (b). Crosses denote parasitoids and filled circles denote the ladybeetles. The grey line in (a) displays the result of the fit to parasitoids, the dashed line is the fit for ladybeetles; in plot (b), the dashed line represents the overall result independent of the biocontrol agent type. Note that all *y*-axis values are partial residuals only containing the information of the temperature dependency and group dependency, excluding the study type as a random effect.

warming (linear term, Fig. 5.3a; Table 5.3), and the hump is narrower for parasitoids (quadratic term, Fig. 5.3a; Table 5.3). In contrast, the biocontrol agent type did not interact with temperature in the capture rate model. Moreover, neither the type nor the squared temperature term contributed sufficiently to explain the data. This reduced to a simple linear temperature model according to the AIC (Tables 5.2 and 5.4). The capture rate increases with an activation energy of 0.57 (Table 5.4; Fig. 5.3b).

Ladybeetles react only weakly to warming, which is in line with earlier studies of predatory terrestrial invertebrates, including other predatory beetles (Rall *et al*., 2010; Vucic-Pestic *et al*., 2011). Hence, this suggests that ladybeetle population dynamics will be dampened within the biologically relevant temperature range. The temperature dependence of parasitoid handling times, however, is much stronger. This result suggests that population dynamics may increase with warming. But this also depends on reproduction rates, prey availability and parasitoid metabolic rates (Fussmann *et al*., 2014). Measuring the temperature dependence of all these biological rates, however, is beyond the scope of this chapter.

Table 5.1. Fixed-effect ANOVA table of the mixed-effects model with the ln-transformed handling time as the dependent variable. *E* is the activation energy of the Arrhenius temperature dependency; E^2 is the activation energy of the square-transformed Arrhenius temperature dependency; type is the biocontrol agent type (ladybeetle/parasitoid). We additionally tested for interactions between type and Arrhenius temperature, as well as the interaction of type with the square-transformed Arrhenius temperature.

Parameter	numDF[a]	denDF[b]	*F*-value	*p*-value
Intercept	1	97	1389.8526	<0.001
E	1	97	17.1153	<0.001
E^2	1	97	58.6483	<0.001
type	1	26	96.1890	<0.001
type:*E*	1	97	3.2686	0.0737
type:E^2	1	97	14.8995	<0.001

Notes: [a]Numerator degrees of freedom; [b]denominator degrees of freedom.

5.5 Insect Outbreaks, Habitat Structure and the Functional Response

One seminal paper on biological control agents and their specific predator–prey dynamics is the spruce budworm outbreak model (Ludwig *et al*., 1978). Ludwig and colleagues aimed to understand insect outbreaks and the underlying biological mechanisms. To simplify the model, they assumed that trees and avian predators lived on a completely different timescale (namely slower) to the spruce budworm. Therefore, they only allowed the spruce budworm population to react numerically (Ludwig *et al*., 1978). The authors chose a type III functional response to model their system (Eqn 5.4), because this type was thought to be the exclusive 'vertebrate' functional response (Holling, 1959b). In contrast to the more general literature (e.g. Oaten and Murdoch, 1975), Ludwig *et al*. (1978) reported that with increasing the quality of growth circumstances for the spruce budworm (e.g. due to a higher standing stock of the spruce), the vertebrate biocontrol agents could no longer manage to control the budworm. This surprising result, however, is only true in the case of a predator whose numerical response to changes in prey availability is significantly lagging behind (i.e. the predator has generation times that are orders of magnitude longer). Hence, more recent studies assuming predators that can react numerically show the exact opposite character. With increasing capture exponent, q, predator–prey dynamics become dampened from limit cycle dynamics to equilibrium dynamics (Fig. 5.4). Small increases in the

Table 5.2. Fixed-effect ANOVA table of the mixed-effects model with the ln-transformed capture rate as the dependent variable. E is the activation energy of the Arrhenius temperature dependency.

Parameter	numDF[a]	denDF[b]	F-value	p-value
Intercept	1	100	74.70882	<0.001
E	1	100	100.37382	<0.001

Notes: [a]Numerator degrees of freedom; [b]denominator degrees of freedom.

Table 5.3. Fixed-effect estimates table of the mixed-effects model with the ln-transformed handling time as the dependent variable. $Intercept_{Ladybeetle}$ is the intercept of the predator group; $Intercept_{Parasitoid}$ is the intercept of the parasitoid group; $E_{Ladybeetle}$ is the activation energy of the Arrhenius temperature dependency of the ladybeetle group; $E_{Parasitoid}$ is the activation energy of the Arrhenius temperature dependency of the parasitoid group; $E^2{}_{Ladybeetle}$ is the activation energy of the square-transformed Arrhenius temperature dependency of the ladybeetle group; $E^2{}_{Parasitoid}$ is the activation energy of the square-transformed Arrhenius temperature dependency of the parasitoid group.

Parameter	Estimate	Std. error	DF	t-value	p-value
$Intercept_{Ladybeetle}$	–4.699399	0.29289798	26	–16.044492	<0.001
$Intercept_{Parasitoid}$	–1.730279	0.30718914	26	–5.632618	<0.001
$E_{Ladybeetle}$	–0.507131	0.13411704	98	–3.781257	<0.001
$E_{Parasitoid}$	–1.252259	0.21612297	98	–5.794195	<0.001
$E^2{}_{Ladybeetle}$	0.153186	0.03116990	98	4.914538	<0.001
$E^2{}_{Parasitoid}$	0.396160	0.05468775	98	7.244028	<0.001

Table 5.4. Fixed-effect estimates table of the mixed-effects model with the ln-transformed, half-saturation density as the dependent variable. *Intercept* is intercept; E is the activation energy of the Arrhenius temperature dependency.

Parameter	Estimate	Std. error	DF	t-value	p-value
Intercept	4.471809	0.6384483	100	7.004184	<0.001
E	0.570934	0.0569870	100	10.018674	<0.001

capture exponent, q (~0.2), have led to stable dynamics (Williams and Martinez, 2004; Rall *et al*., 2008; Kalinkat *et al*., 2013b). Notably, this stabilizing effect of a type III functional response also holds for large food webs (Williams and Martinez, 2004; Rall *et al*., 2008). Beside the classical idea that type III functional responses occur only if the predator is a rather 'intelligent' vertebrate, recent studies have also found type III functional responses for invertebrate predators (Aljetlawi *et al*., 2004; Sarnelle and Wilson, 2008). Moreover, adding habitat complexity in the experimental set-ups facilitates the occurrence of type III responses by introducing prey refuges (Vucic-Pestic *et al*., 2010b; Toscano and Griffen, 2013; Kalinkat *et al*., 2013b). Together, the modelling results suggest that it is desirable that biocontrol agents should show a type III functional response to assure a constant control of invertebrate pests. But the current methods to analyse and obtain empirical functional responses from laboratory studies should be questioned. By analysing a subset of terrestrial invertebrates of the functional response database from Rall *et al*. (2012), we found that 293 out of 313 documented functional responses were type II and only 20 were of type III (Fig. 5.5a, $q > 0$). This might partially be a result of the fact that about 60% of all functional responses were measured without any environment (124 with and 189 without habitat structure, Fig. 5.5b). Habitat structure increases the probability of an increase in capture exponent by 0.12 (s.e. = 0.023; t-value = 5.257; p-value < 0.001; Fig. 5.5d). This is disillusioning, as already a small amount of moss in functional response arenas might change the outcome of the experiment greatly (Vucic-Pestic *et al*., 2010a). Another possible explanation is the insufficient range of prey densities not allowing for a correct statistical analysis (Sarnelle and Wilson, 2008). Another step in the right direction would be to extend functional response settings to greenhouse settings, or even to field mesocosms. This, however, has only been done three times out of a total of 313 studies (Fig. 5.5c), probably because it poses enormous logistical challenges and means labour-intensive work. Habitat structure, however, is not the only driver that shifts a type II to a type III functional response. Moreover, the combination of habitat and an increase of body mass ratio increases the capture exponent (Fig. 5.6; Vucic-Pestic *et al*., 2010b; Kalinkat *et al*., 2013b). In another study, the structure of the habitat of the pest prey and the control predator was changed qualitatively between different crops (De Clercq *et al*., 2000). There, the feeding rates of predatory Pentatomids on beet armyworms were tested on three different host plants – aubergine, sweet pepper and tomato. The change of habitat can cause a shift from a type II functional response (aubergine, sweet pepper) to a type III response (tomato) and, moreover, also dampen the overall maximum feeding rate (Fig. 5.6a). The authors discuss that this might be due to the structural effect of the glandular trichomes of the tomato.

The most extreme differences may have been shown by Vucic-Pestic *et al*. (2010a), where the functional response not only shifts, due to the inclusion of habitat structure, but also the overall feeding rate drops by ~75% over the whole range of measured prey densities (Fig. 5.7b).

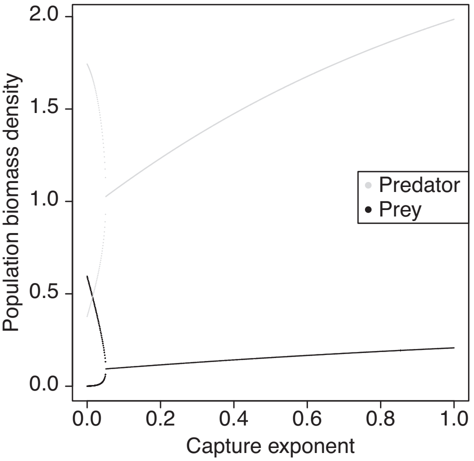

Fig. 5.4. The change of population dynamics due to a shift in the q exponent. A bifurcation diagram showing how population dynamics change due to an increase in the q exponent. The points display the minima and maxima of a single time series at a given q exponent.

5.6 Discussion and Conclusion

Functional responses, or more generally the strength and shape of feeding interactions, determine the stability of predator–prey pairs up to whole ecosystems (Williams and Martinez, 2004; Rall *et al.*, 2008). Due to this theoretical background, predator–prey functional responses have drawn attention from a wide range of research fields in ecology (Hansen *et al.*, 1997; Skalski and Gilliam, 2001; Jeschke *et al.* 2002; Englund *et al.*, 2011; Rall *et al.*, 2012; Pawar *et al.*, 2012). Beyond this branch of basic research, the conceptual framework has been especially well received in the investigation of the natural control of insect pests, from its very introduction in the 1950s all the way to modern applied ecology (e.g. Beddington *et al.*, 1978; Dixon, 2000). However, the correct determination and evaluation of predatory functional responses, particularly from an applied biological control perspective, is not as straightforward as we might wish: the experimental assessment can be done under natural conditions, but the correct

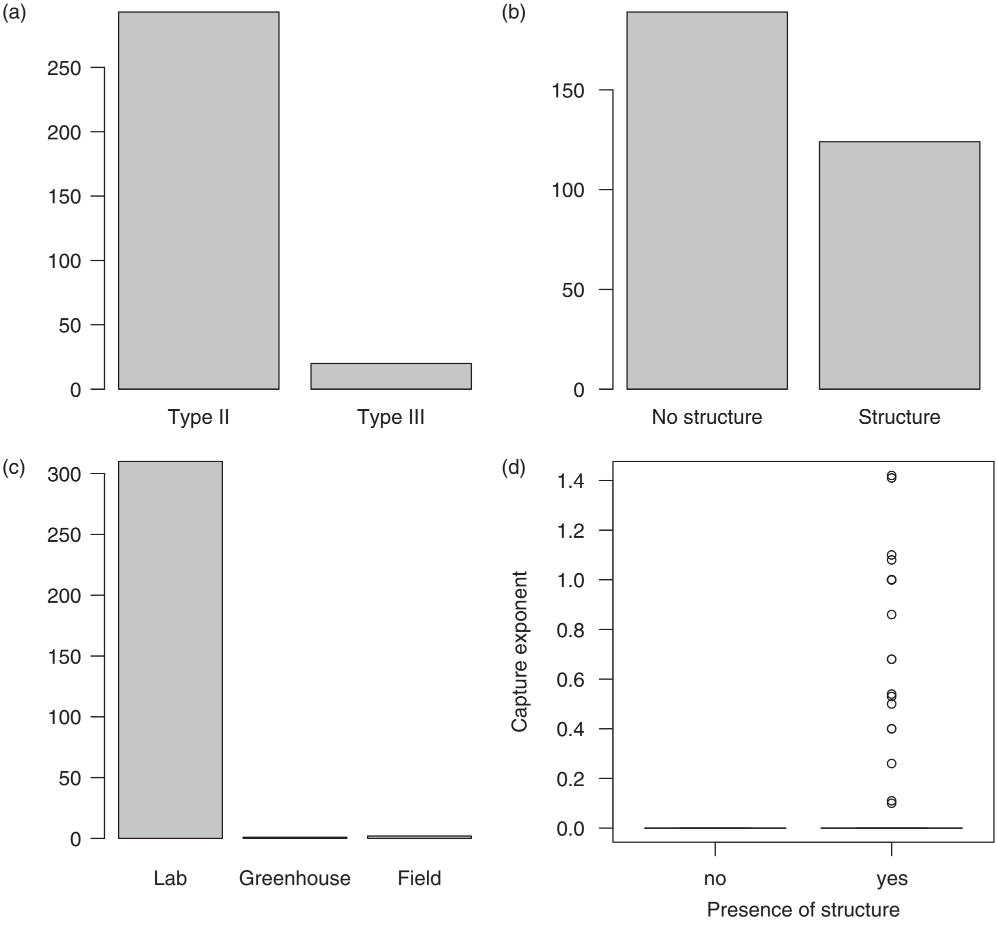

Fig. 5.5. Structure and type of functional responses. The number of functional responses that were type II or type III ($q > 0$) (a); the number of functional responses that were measured with and without habitat structure (b); the number of functional responses that were measured in the laboratory, greenhouse or field (c); the effect of habitat structure on the q exponent (d).

documentation of feeding events is very labour intensive (e.g. video surveillance; Schenk and Bacher, 2002) and often almost impossible for diminutive organisms in complex habitats. The other way to deal with such hardships is to apply standardized, simplified experimental set-ups in the ‘clean laboratory world’. In the biological control literature, for instance, a standardized way to measure functional responses is by documenting the predation events on leaf disks in small Petri dishes (e.g. Munyaneza and Obrycki, 1997; Koch *et al*., 2003). Moreover, the number of laboratory studies of invertebrate functional responses outnumbers field studies enormously, while laboratory set-ups including complex habitat structure are found in lesser numbers than studies in simplified, unstructured systems. Fortunately, however, there are now certain studies where the effects on feeding rates have been directly compared between simplified and complex structured habitats for different terrestrial invertebrates (e.g. Munyaneza and Obrycki, 1997; Hohberg and Traunspurger, 2005; Hauzy *et al*., 2010; Vucic-Pestic *et al*., 2010a; Kalinkat *et al*., 2013a). But, there is still a need to define improved standards to measure functional responses, such as including habitat structure, a sufficiently large arena size and extended prey density ranges, to avoid artificially biased results.

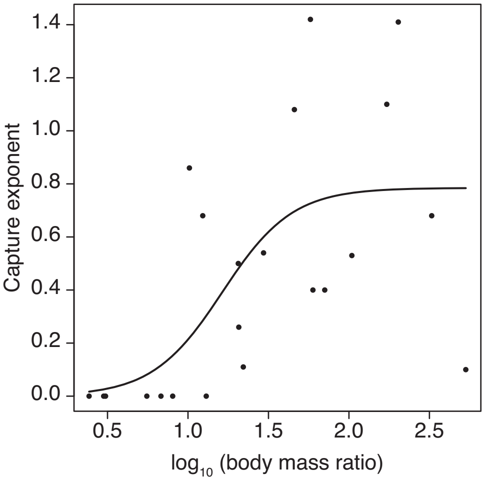

Fig. 5.6. The *q* exponent increases with the body mass ratio. (All data were from Vucic-Pestic *et al*., 2010b. See Section 5.3.)

Our results on the temperature dependence of functional responses suggested contradictory results. Ladybeetles showed the same weak increase in temperature as other terrestrial invertebrates (Rall *et al*., 2010; Vucic-Pestic *et al*., 2011), whereas the reaction of the parasitoids to changes

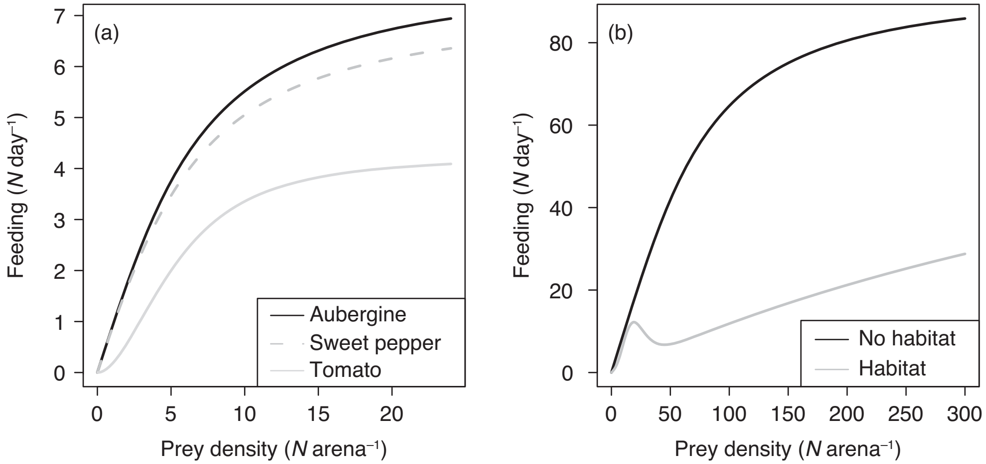

Fig. 5.7. Structure and type of functional responses. Effects of plant host type on the performance of the biocontrol agent (a; De Clercq *et al*., 2000). Spider feeding is influenced by the presence or absence of moss (b; Vucic-Pestic *et al*., 2010a).

in temperature was more pronounced. Together, both results suggest contradictory outcomes for population dynamics. However, as one recent study has shown, we urgently need to gather and integrate more knowledge on other biological rates such as metabolism or fecundity, and their respective ratio, to be able to make predictions (Fussmann *et al*., 2014). Besides the analyses of habitat structure and the temperature dependence of functional responses, no studies have yet analysed the interactive effect of both.

Here, we reanalysed existing data and discussed how two global change drivers, habitat loss and temperature, affect the strength and shape of consumer–resource functional responses. Results on temperature dependence were inconsistent, allowing one to suspect that interaction strengths in the long term might decrease, and thereby reinforce population stability. Habitat structure and complexity interactively change a type II to a type III functional response, which is known to increase population stability. By reducing habitat structure and complexity due to climate change, we assume that stability might decrease due to habitat loss. As there are no studies investigating the combined effect of both, change in temperature and habitat, we may only be able to guess that both effects may cancel each other out. Future studies should urgently address this combined effect of habitat and temperature. Ideally, these studies should not only estimate feeding rates but also other biological rates, to make better predictions on the performance of biocontrol agents in the shade of global change.

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6

Physiological Variation of Insects in Agricultural Landscapes: Potential Impacts of Climate Change

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Abstract

Understanding the physiological and behavioural responses of insects to climate variation is critical, for several reasons, of which three are perhaps most important. First, developing a deeper understanding of pest population dynamics and postharvest control requires information on thermal (and other environmental) traits. Second, invasion of new and emerging pests into novel environments requires some knowledge of the basics of environmental physiology. Finally, to predict and manage aspects of efficacy in control programmes through the release of laboratory- or mass-reared insects typically hinges on some information from phenotype–environment interactions. Here, we provide an overview of how climate and landscape environmental opportunities vary spatially and temporally in order to quantify better ecologically meaningful microclimates for insects and to understand better behavioural opportunities in agricultural landscapes. Then, we describe several key biogeographic patterns that may be significant from an insect pest/climate change perspective, and then discuss briefly possible mechanisms associated with variation in the physiological tolerance and performance of insects. We review and discuss issues surrounding the prediction of climate change and insect physiological and behavioural responses, and consider how insect pests might be impacted by changes in climate in the future via physiological tolerances. Next, we consider movement and dispersal in agricultural landscapes, and what this may mean for recolonization potential or introduction to novel environments under climate change scenarios, especially given how many of these processes are influenced by climatic factors. Finally, this chapter examines interactions between hosts and biocontrol agents, and how climate may influence the outcome of these interactions. The chapter concludes with a summary and discussion of possible areas for future research and key themes emerging from this review of physiological variation in agricultural landscapes and the potential impacts of climate change.

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6.1 General Introduction

There is increasing concern surrounding the responses of insect pests to climate change. Given the agricultural and economic burden imposed by several notorious crop pests, this concern is indeed warranted. In some environments, the presence of a pest can be a hindrance to transformation from poverty for subsistence farmers, particularly in developing countries, while in the case of others it may mean the limitation of, or wholesale banning from, various export markets. This chapter seeks to review the relevant literature on the potential climate change responses of insect pests for the layperson who may have an agricultural background but little to no knowledge of insects or their environmental physiology. Here, we cover aspects of climate and its variation across agricultural environments, including the planet more broadly. We then discuss behavioural regulation by insects and the avoidance of detrimental abiotic conditions, and then give a primer on insect physiological variation more generally. This is not meant to be an exhaustive review on insect physiology since many excellent, more detailed insect physiology and biochemistry texts exist already (e.g. Chown and Nicolson, 2004; Lee and Denlinger, 2010; Harrison *et al*., 2012). We then touch on the movement and dispersal of insect pests in agricultural environments and how it might be affected by climate change, and finally we discuss interactions between hosts and biocontrol agents or their natural enemies. We conclude with a few general points of consideration for key future directions and some of the major issues highlighted in this chapter (e.g. spatial and taxonomic bias in the knowledge of insect responses to climate change).

6.2 Climate and Landscapes – Temporal and Spatial Variation

The availability of abiotic resources, such as solar radiation, temperature and moisture, and hence any opportunities for the growth and persistence of insects in agricultural landscapes, are sporadic across the surface of our planet. Moreover, these are strongly modified in several crop types by agricultural practice (e.g. the addition of water through crop irrigation). Generally, temperatures are warmest at low latitudes and coolest at high latitudes or altitudes, while moisture availability has a less systematic pattern with spatial position. Consequently, several bioclimatic regions have been well characterized (Metzger *et al*., 2013; Plate 1). Typically, one or a few key insect pest species are associated with a particular bioclimatic region, generally thought to be associated with physiological and developmental requirements for survival and optimal reproduction (e.g. Andrewartha and Birch, 1954).

Strong seasonal patterns in weather, especially in the northern hemisphere and to a slightly lesser extent in the southern hemisphere, can result in patterns of annual cycles in pest population growth and decline. In some insect pests, these cycles are also closely linked to growth cycles of the host plant. The absence or excess of only a single, key variable, such as moisture, may, however, be sufficient to reduce the probability of the establishment of an insect pest or biocontrol agent effectively to zero. The challenge of forecasting climate change impacts in agricultural landscapes are to link functional insect traits (e.g. development threshold or sufficient time spent above a key limiting low temperature threshold, reproductive output, locomotor speed or other key predictor traits) with variables of climate that are in some way determining (or limiting) for population growth, or perhaps other aspects of climate that result directly in population-level mortality (e.g. high temperature extremes).

Here, we focus on aspects of the processes of key population dynamics, making use of the general equation that local population growth rate = (birth rate + immigration) – (death rate + emigration) (e.g. Hargrove, 2004). For convenience, we examine factors that influence growth and survival together, and death separately, while movement (immigration and emigration) is treated as a single section on dispersal.

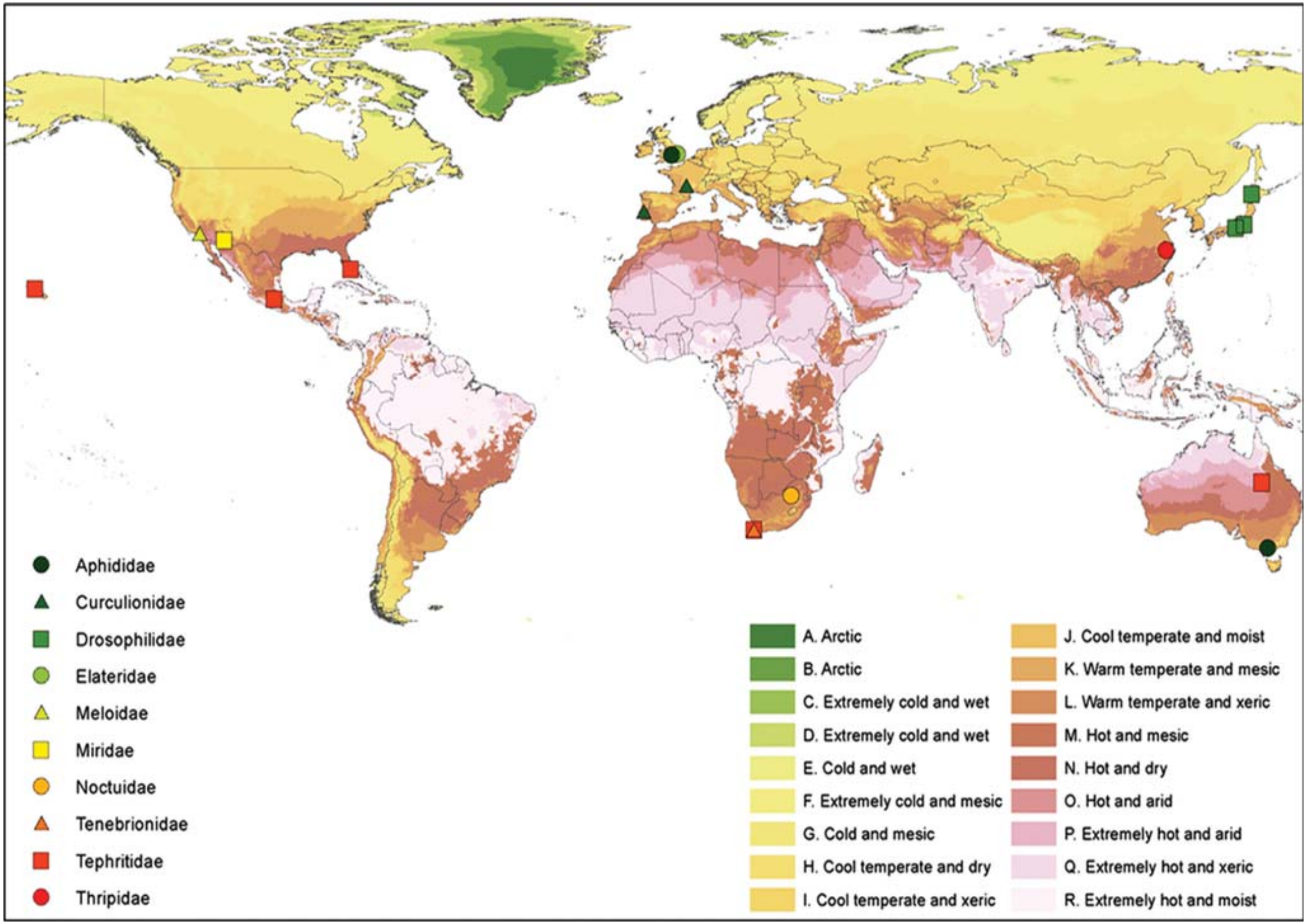

Plate 1. A global map showing bioclimatic zonation including sampling localities of those families included in the thermal limits data set used in this chapter. (From Metzger *et al.*, 2013.)

A different abiotic factor (or suite of factors) may be responsible for population establishment and increases in abundance as compared to those causing population declines. For example, a lower threshold temperature may be important for initial population growth, but just because this threshold is continuously exceeded does not necessarily mean populations will continue to grow exponentially, especially if another factor (e.g. water loss rate or energy consumption) increases at a faster rate. Climate or niche requirements can therefore be described on several axes (e.g. Elith *et al*., 2010), and the number of axes may vary between insect pests possessing different biology. Another key challenge is to understand the behavioural regulation of microclimate conditions, as this may decouple the association of body temperature to air temperature, the latter of which is typically the principal variable included in forecasting or modelling efforts. Here, we present an overview of some of the key factors potentially influencing the forecasting of insect responses to climate change and some of the general patterns that emerge from examining climate variation. Given the propensity of the current literature, much of the focus is on thermal responses, although in reality, moisture availability and probably also synergistic or multiplicative interactions among different abiotic factors (e.g. nutrient availability; Coggan *et al*., 2011) are likely to be critical determinants of pest population dynamics, too (see review in Chown *et al*., 2011). Despite the strong focus on thermal effects for insect pests, this is not meant to be an exhaustive review of thermal biology, since many excellent introductory texts are readily available (e.g. Heinrich, 1993; Chown and Nicolson, 2004; Lee and Denlinger, 2010). Instead, we discuss key principles, and a few recent examples of their potential value in understanding pest responses to climate change, and give an overview of the current literature and some potential future directions, and thereby address the main focus of this chapter.

Climate change involves complex concurrent changes in many environmental variables. The average global surface temperature has increased by roughly by 0.6°C in the past 100 years and is predicted to increase even further, with an accompanying rise in carbon dioxide (CO_2) levels and a change in precipitation (IPCC, 2013). Insects are poikilothermic and they are therefore influenced markedly by weather and climate. The effect of climate change on insect pests can be indirect, with changes associated with climate interceded by other factors; namely, the host plant or direct, all of which may influence behaviour and physiology (Porter *et al*., 1991; Bale, 2002). If conditions experienced by the insect change beyond that with which the insect is able to cope, they may respond in one or a few different ways. There are at least three major mechanisms important in responding in the short term to a changing climate; these include microevolutionary change, dispersal and phenotypic plasticity (Pulido and Berthold, 2004) and are not necessarily mutually exclusive. A typical example of dispersal change is shifting the species' range boundaries, which is commonly limited by low temperature thresholds, especially in the northern hemisphere. The capacity of a species to shift its range depends, however, on the species' ability to colonize and establish a new population (Angert *et al*., 2011). Dispersal permits organisms to colonize new suitable habitat (Broquet and Petit, 2009), and it is thought that the link between dispersal and gene flow may be an essential component of adaptation to changing environmental conditions (Kokko and López-Sepulcre, 2006). These are especially important considerations in the light of global climate change as they affect a variety of factors important for the management of insect pests in the agricultural landscape.

6.2.1 Quantifying ecologically relevant microclimates

Ecological studies have traditionally used broad-scale meteorological data sets, relating macroclimate conditions to the abundance and distribution of pests (Andrewartha and Birch, 1954). While such studies may yield a general indication of climatic factors that limit a species' survival, they do not necessarily represent conditions experienced by the organism in question (Helmuth *et al*., 2006). Meteorological climate data are generally recorded at 2 m above the ground; however microenvironments of pests can vary substantially from these measurements (Woods et al., 2014). In an apple orchard, for example, ambient temperature and wind speed vary with height above the substrate, whether it is below, above, or within the trees canopy (Fig. 6.1). Surrounding vegetation may similarly alter local temperature, humidity, radiation and wind speed, while the slope and aspect of an orchard affects direct solar radiation loads (Campbell and Norman, 1998).

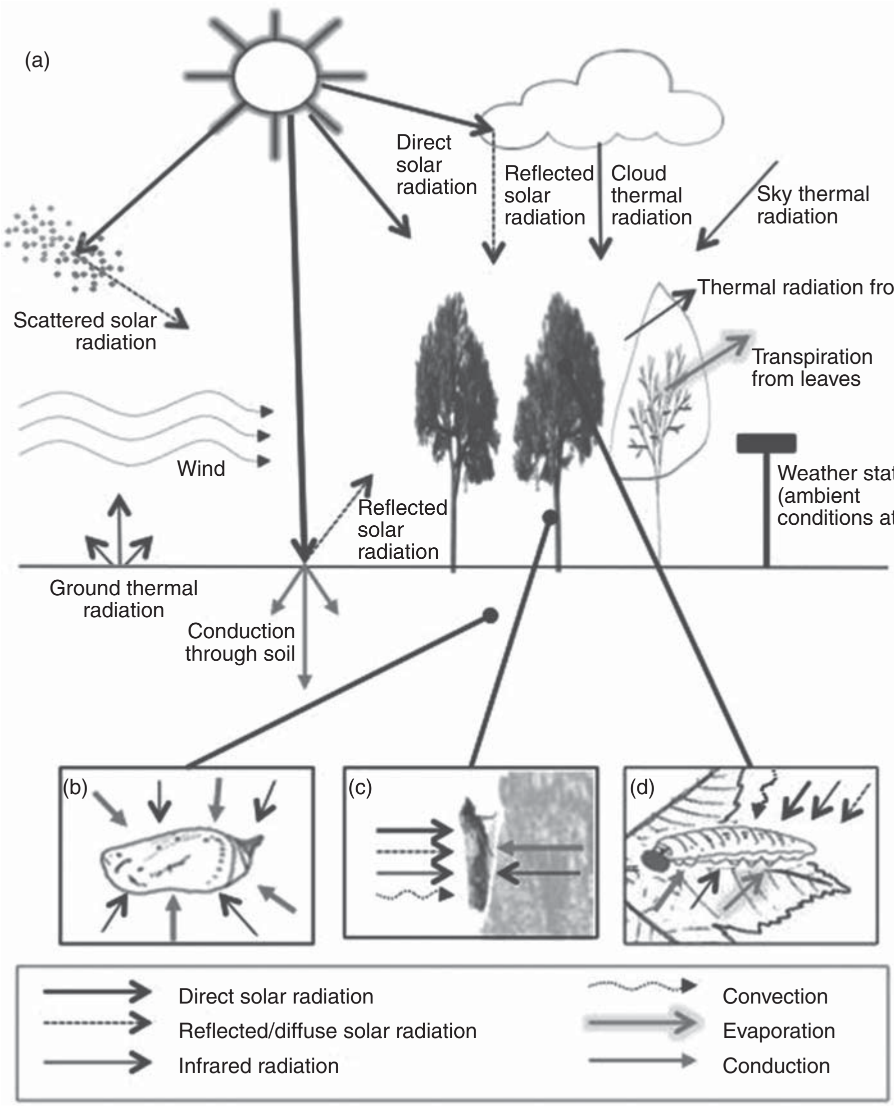

Fig. 6.1. Schematic diagram of the flow of (a) heat and energy within an orchard. Exchange of heat between a (b) pupa, (c) adult and (d) larva lepidopteron pest, and their respective microclimates (soil, tree trunk and leaf), are shown. Arrow direction and style indicate the direction and process of heat flow, respectively.

Insects can occupy a wide range of microenvironments within a particular orchard or crop system. Typically, these include, but are not limited to, the leaf foliage or canopy parts, which in some crops may be several metres off the ground, under the bark on tree trunks, or within the roots and soil. Indeed, some insect pests, especially those feeding on tubers, spend much of their life below ground. The ambient conditions within all of these sites, and even in adjacent areas, may vary quite substantially from one another (Fig. 6.1), providing opportunities for pests to buffer temperature stress.

For plant-dwelling pests, the host plants they inhabit largely dictate the microenvironments. Describing such microenvironments is particularly complicated because the host plant responds to, and thus modifies, the surrounding abiotic conditions (Pincebourde and Casas, 2006). Stomata in leaves, for example, open or close to regulate vapour pressure, temperature and CO_2 and water content of the tissue (Boulard *et al*., 2002). Such physiological changes in turn affect the boundary layer of the leaf and, consequently, the humidity and temperature experienced by animals on its surface. Furthermore, many insect pests have the capacity to actively construct their own environment within the plant (e.g. galling insects), which in turn changes the ecophysiological properties of the plant tissue (Miller *et al*., 2009). Using a combination of empirical data and model predictions, Pincebourde and Casas (2006) showed that the temperatures within mines created by a leaf-mining insect (*Phyllonorycter blancardella*) were significantly hotter than surrounding, undamaged leaf tissue. Herbivores also induce damage while feeding on leaves, which can result in elevated leaf temperatures (Pincebourde and Woods, 2012). Describing the microenvironments of the different life-history stages of leaf-dwelling pests therefore requires not only an understanding of the local climate but also the interactions between the host and its pest.

Such fine-scale biotic interactions can in turn buffer or exacerbate broad-scale spatial and temporal patterns in climate. While temperature and humidity vary in a systematic manner with latitude, if plants adapt to their local conditions to optimize fitness, pests may be buffered from geographic variation in climate (Helliker and Richter, 2008). On the other hand, long-term increases in temperature occurring through time may be exacerbated if pest species continue to modify their host plant tissue so that it hinders the plants' thermoregulatory capacity (Pincebourde and Woods, 2012).

To describe the microenvironment of a pest, a biophysical model may be employed: this refers to a set of equations, based on the first principles of heat and mass balance physics, which translate broad-scale meteorological data sets into the conditions experienced by the organism in question (Gates, 1980). Developing a biophysical model relies on specific information regarding the animal's habitat and behaviour; in the case of a leaf-dwelling organism, this involves the complicated processes of host plant physiology (Pincebourde and Casas, 2006). None the less, integrating such microclimate models into studies that aim to predict climate change responses, rather than simply assuming a direct correlation between macroclimates and species distributions, will invariably yield more accurate predictions.

6.2.2 Behavioural opportunities in the agricultural landscape

Understanding how climate change will affect insect pests requires not only an understanding of the available microenvironments but also the animal's capacity to exploit them. For an insect pest with a holometabolous life cycle, the capacity to buffer temperature stress through behaviour will vary between the different life-history stages: highly active adults are more readily able to utilize microclimatic temperature variation in comparison to their relatively more sessile (and immobile) immature stages. In many cases, the survival and development rate of the eggs and early larval instars are ultimately dependent on the site of oviposition chosen by their mother.

For example, laboratory assays show that gravid females of the oriental fruit moth (*Grapholita molesta*) preferentially lay eggs under the most optimal thermal conditions for offspring development and size (Notter-Hausmann and Dorn, 2010). These patterns have also been observed in the field, where female moths oviposit more readily on the sunny side of plants at cooler ambient temperatures (Bernays and Chapman, 1994). However, as larvae develop into older, larger instars, thermoregulatory capacity often improves. Final instar codling moth larvae, for example, can regulate their core body temperature relatively well by selecting warm or cool sides of their host apple; again, likely to optimize growth and development (Kuhrt *et al*., 2005). These larvae may also dictate thermal conditions encountered during metamorphosis by selecting either the northern or southern aspect of a tree trunk on which to pupate. Therefore, depending on the species, the life-history stage and microclimate heterogeneity, agricultural insect pests will vary in their capacity to buffer potential temperature stress behaviourally. This in turn complicates any modelling efforts and the ability to predict core body temperature, and hence fitness. While only a few studies have incorporated behavioural thermoregulation parameters into the mechanistic models described above, doing so will invariably yield more accurate and relevant predictions of how climate change will affect pest distribution and abundance.

Measuring and estimating field body temperatures remains a major challenge in understanding the climate change responses of insects. In most cases, species are assumed simply to experience air temperature, and the validity of this assumption naturally depends on the species in question. Several methods exist for determining insect body temperatures, including insect pests, but these are typically based on radiotelemetry, which has a lower mass limit that is considerably larger than many pest species. An alternative approach is to undertake molecular telemetry (Feder *et al*., 2000), in which a particular gene or protein response is calibrated under controlled laboratory conditions with a particular abiotic stressor (e.g. temperature) and then measured in free-roaming individuals to then infer stress that potentially was experienced under field conditions. This approach is, however, challenging, since it requires strong background knowledge of the biochemical process investigated and may be confounded by other factors (e.g. age-related changes in gene expression). Nevertheless, it holds considerable promise, especially with the decreasing costs of high-throughput DNA and RNA sequencing, and is presently underutilized.

6.3 Thermal Physiological Tolerance and Performance

Insects, like lizards and amphibians, are ectotherms. Rather than producing heat through metabolic processes and maintaining their own internal body temperatures as mammals and birds do, they are more reliant on the external environment to maintain function. As such, every stage of their life cycle and everyday functioning is generally subject to the abiotic environment that they inhabit (Fig. 6.1). Insects function optimally within a certain thermal window, and this window can differ markedly among species, and even life stages. Predicting pest species responses to temperature is important for two key reasons. First, the timing of key life history and population dynamic events significantly influences when to anticipate crop losses and optimally apply control methods, e.g. pesticide use. Second, once the pests have emerged, temperature greatly influences their ability to forage, disperse and mate, therefore influencing their potential to cause damage.

Key life-history traits such as development time, longevity and fecundity are influenced by temperature, with colder temperatures generally slowing an individual's growth rate and prolonging their lifespan. The timing of these events is generally referred to as the phenology of the species. From a pest perspective, these life-history traits influence the population dynamics of the insect greatly. For example, a faster growth and maturation rate, and a higher reproductive output, results in a higher turnover in pest numbers, therefore potentially causing more damage to the crop over time. Identifying the timing of peak abundance is particularly important for devising strategies to control agricultural pests, especially the effective application of insecticides. This is the premise of 'day-degree' models, used for predicting the timing of the pests' peak abundance. These models are used to calculate the approximate emergence times of pest species by taking into account their development time and the role that temperature plays in slowing down or speeding up the process (e.g. Barton and Terblanche, 2014). A certain number of days above a temperature threshold are required to complete development. Once this threshold is determined for a particular species, then temperature data from the current season can be compared to estimate an emergence date. Control methods, generally pesticides but also orchard sanitation, can then be applied prior to emergence or directly on to developing larvae, depending on the life stage that causes the most damage. Even the most basic day-degree model contains significant predictive power and reduces the unnecessary use of chemicals. The effectiveness of these models, however, is limited by the quality of the information used to generate them; more accurate details of thermal limits or of the thermal microenvironment experienced by the species will typically be beneficial. The level of information required by a particular model depends on the model's predictive ability to meet a specific purpose.

The activity or performance of insects, i.e. foraging, flight, mating, etc., is influenced greatly by thermal conditions, and in a very similar pattern to that seen in biochemical reaction rates (Huey and Stevenson, 1979; Kingsolver, 2009). The performance curve illustrates the relationship between temperature and the activity of a single insect or a population of individuals (Angilletta, 2009). It is generally considered that the performance curve represents a trade-off over evolutionary time between specialists (with a high, narrow curve) and generalists (with a lower, broader curve; Fig. 6.2). As such, the height and breadth of the curve are sometimes important considerations, especially in the choice of a suitable biocontrol agent for a particular pest. If temperatures extend below or above the performance thresholds, broadly defined as the critical thermal minima (CT_{min}) or the critical thermal maxima (CT_{max}), respectively, then the insect cannot function and may enter a coma-like state. This coma state may be reversible if exposure is short; however, their chance of survival decreases substantially over time, especially the greater the temperature that exceeds their critical limits. These lethal limits (ULT and LLT for upper and lower lethal temperature limits, respectively) are generally not determined for single individuals but rather as a ratio of a cross-section of individuals and denoted, for example, as the LT_{50}, the temperature where exposure resulted in mortality for 50% of the population. From the CT_{min}, performance improves exponentially with increasing temperature until reaching peak performance, known as the thermal optimum (T_{opt}), before declining rapidly towards CT_{max}. As such, the performance curve is asymmetric, with the T_{opt} generally closer to CT_{max} than CT_{min}. As a result, ULTs generally exist close to the performance limit and there is greater variation for lower performance limits, such that there are several strategies for dealing with cold temperature stress. Freezing tolerance is a defining physiological trait for cold tolerance and is characterized by the temperature at which an individual freezes (known as the supercooling point; Denlinger and Lee, 2010). These freeze-tolerant species generally possess physiological adaptations that reduce the build-up of ice crystals in their cells that cause physical damage. Typically, freeze-tolerant insects freeze at warmer temperatures than freeze-intolerant species, allowing their cells to freeze before accumulating damage and effectively 'waiting out' the frost until conditions improve, whereas freeze-intolerant species eventually succumb to the cellular damage. This adaptation is likely to be important in the northern hemisphere in particular, where winter temperatures are far more severe. Tolerating these extreme cold events is likely to place

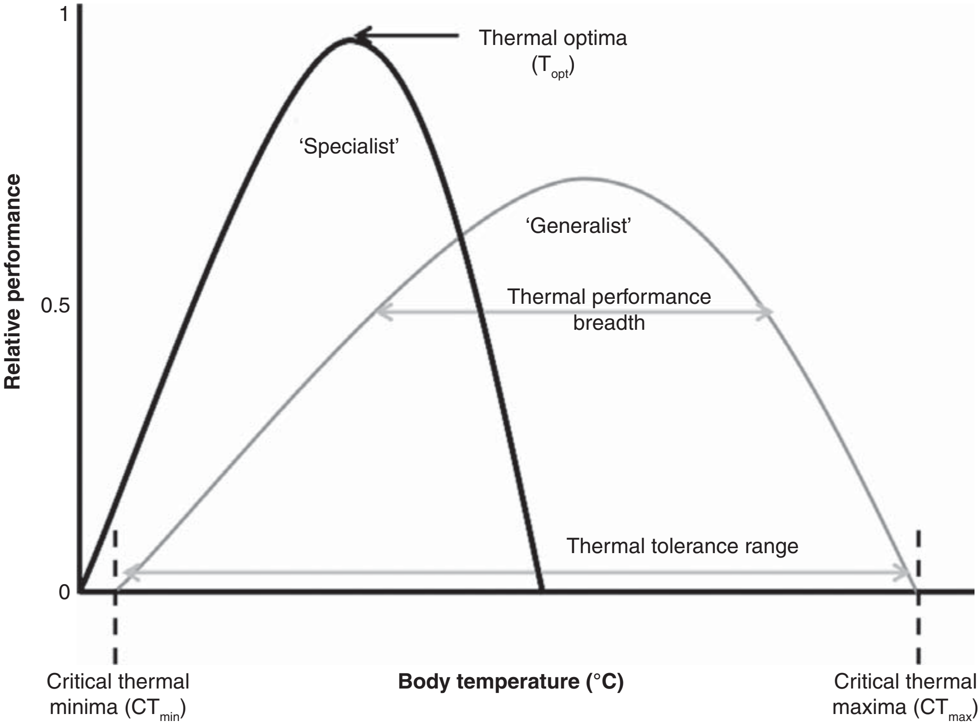

Fig. 6.2. Theoretical thermal performance curve for a thermal generalist (grey) and specialist (black). A generalist individual or species may remain active across a broader range of thermal conditions, and therefore have a broader tolerance range than a specialist. However, a specialist will have a much higher relative performance at the temperature they are closely adapted to, thereby providing a potential fitness benefit.

an important restriction on the distribution of pest species.

6.3.1 Thermal tolerance and geographic distributions

The shape of pest species thermal performance curves places important restrictions on the thermal conditions, and therefore habitats, in which the insect may function successfully. As such, they provide a useful tool for investigating thermal environmental thresholds that potentially could limit species distributions. Theoretically, the breadth of an individual's performance curve will match the average thermal fluctuations in the environment closely, as the costs to reproduction and survival of exceeding these critical thermal limits would not be sustainable (Lynch and Gabriel, 1987; Gilchrist, 1995). Using this same logic, species' thermal optima should also match the mean environmental temperature. Both of these predictions have been proven using mathematical modelling; however, it is difficult to test using natural populations. In general, it is difficult to obtain accurate estimates of thermal limits to life history and performance traits in ectotherms in their natural environment, as there are many other abiotic and biotic factors that may interact with and potentially influence estimates, as stated earlier. In order to counter this potential bias, many thermal tolerance assays focus on a single element, i.e. upper or lower thermal limits, and are conducted under controlled laboratory conditions.

Using laboratory estimates to extrapolate to natural conditions may seem oversimplified; however, there are many situations where comparisons conducted in the laboratory can be matched to patterns of, for example, geographic distributions observed in nature (Addo-Bediako *et al*., 2000). This can be achieved by comparing populations of the same species from different locations with very different local environmental conditions. A well-known and widely used example of environmental variation is the latitudinal cline in temperature across the Earth. Broadly speaking, temperatures at the equator are warmer and more stable than at either the North or South Poles. Therefore, as latitude increases, the average temperature decreases and becomes more seasonal, creating an associated thermal gradient. Species with broad distributions that encompass a range of latitudes should exist across a variety of different conditions, with natural selection presumably shaping local populations to maximize their fitness with their environment. This is evidenced by the linear associations of traits such as chill-coma recovery time (with faster recovery in high-latitude populations) and heat knockdown time (with higher tolerance in low-latitude, tropical populations) in *Drosophila melanogaster* populations (see, for example, Fig. 1 in Hoffmann *et al*., 2002). There are many other examples of clinal association studies in *Drosophila*, particularly with transects that run the length of the east coast of Australia and the west coast of North America. In general, the association of tolerance traits with environment are found as expected; however, the strength or shape of the relationship may change over time, indicating that selection pressures may change seasonally or vary in intensity over time or among life stages.

The association of thermal physiology traits with environmental gradients, such as those illustrated in clinal studies, only provides a limited understanding of the environmental factors that influence species distributions. As there are many environmental variables that change with latitude (i.e. temperature, rainfall, humidity, etc.), any one or a combination of these factors may contribute to the patterns observed. Also, the traits generally measured are easy to test in a laboratory setting but may have limited applicability in the natural environment. In order to assess the applicability of laboratory assays to natural environments, it is necessary to corroborate these results with an estimate of field fitness/performance. This was first achieved in *D. melanogaster* by acclimating individuals at temperatures known to be beneficial to thermal tolerance under laboratory conditions, marking them with fluorescent powder and then releasing them in a resource-poor location (Kristensen *et al*., 2008). The number of individuals from the different treatments recaptured at food bait stations can then be correlated to environmental conditions and compared with results from laboratory estimates. In this instance, flies acclimated at cool temperatures performed best under cold days in the field, both in Australia and Denmark (Kristensen *et al*., 2008). Similarly, flies exposed to warmer conditions performed best only under warmer conditions. In both cases, the prior thermal exposure gave an advantage in that environment on subsequent exposure, but came at the cost of poorer performance in the opposite kind of environment (i.e. cold exposure penalized performance at warmer conditions and vice versa).

The *Drosophila* spp. used for laboratory studies, while not significant pests (although, see emerging invasive pest, *Drosophila suzukii*), are important model organisms for studies linking physiology with distributions and environmental variables. They are short-lived and easy to rear under laboratory conditions, allow extensive, detailed studies and, particularly for *D. melanogaster*, are replicable in many parts of the world due to their cosmopolitan distribution. Studies on these model organisms may also provide the backbone for developing new technology and understanding natural processes that are transferable to other, non-model organisms, such as the evolution of insecticide resistance. The methods already developed, such as the field performance protocols described by Kristensen *et al*. (2008), are important for application to pest species, particularly for the population control method of the sterile insect technique (SIT). This method uses the release of mass-reared sterile insects to mate with wild individuals, and thus aims to decrease local density to a threshold from which the population is unable to recover. Rearing large colonies of pest species to be irradiated and released into natural environments is costly, and therefore needs to work effectively. If prior exposure of laboratory- or mass-reared individuals to the external temperatures allows them to perform better than the males of local populations, then released individuals can be better tailored to match local populations at a particular time, perhaps resulting in more efficient pest control. This may not always be effective, however, and needs to be assessed on a case-by-case level. For example, Chidawanyika and Terblanche (2011) showed much larger recapture rates of laboratory-reared male codling moth, *Cydia pomonella*, in cold environments following prior acclimation at cooler temperatures; however, these individuals were recaptured at much lower rates than warm-acclimated moths (i.e. performed badly) under warmer conditions. By combining laboratory and field estimates together with new techniques developed on model organisms, more effective protocols for controlling pest species can be developed and implemented.

6.3.2 Climate change and pests

Given that there are several ways in which species can respond to climate change, and mainly in anticipation of a generally warmer and drier environment predicted through climate change general circulation models (IPCC, 2013), insect species may shift their geographic distributions or phenology in an attempt to track changes in their optimal conditions. Within ectotherms and endotherms alike, there is substantial evidence to suggest that range shifts are already occurring, particularly towards the poles, where temperatures are increasing; with recent evidence also suggesting this is the case for pest species (Bebber *et al*., 2013). There are several reported cases of phenological change with environment in insect pests. The broader impacts of such phenological change are, however, largely unclear. For example, a strong negative impact of climate change may occur when there is a mismatch between the timing of insect life-history events and those of their host plants, i.e. peak flowering, nutrient production, etc. (Visser and Holleman, 2001). This has been observed to great effect in the early egg hatch of winter moth (*Operophtera brumata*), arriving before the bud burst of the oak host plant and resulting in the starvation of that cohort of individuals (Visser and Holleman, 2001). Although these impacts are less well documented for pest damage on the crop or host, they may have subtle effects on other aspects of pest management, such as biocontrol efficacy, or predator–prey interactions. For agricultural pests, studies have detected a mismatch in phenology between the pest and their natural enemies, such as the cereal leaf beetle, *Oulema melanopus*, and the parasitoid wasp, *Tetrastichus julis* (Evans *et al*., 2013). The wasp parasitizes the eggs of the beetle, resulting in a reduced population size of the beetle. However, in warmer spring conditions, beetle eggs hatched before they were parasitized, reducing the effectiveness of biocontrol methods for this pest (Evans *et al*., 2013).

Another major concern of climate change for pest species is the potential for higher crop damage through an increased number of generations within an agricultural season (voltinism). Based on a day-degree model, an increase in the number of suitable days for development could allow faster generation time and, therefore, an additional generation (or possibly even two) to develop within a growing season (e.g. Barton and Terblanche, 2014). The possibility of this change would be determined by the factors that normally limit population sizes, such as the availability of a food source and also whether the species exhibits overwintering strategies, i.e. has dormant (diapausing) life stages during cold winter months. Model predictions for the non-diapausing moth, *Plutella xylostella*, indicate an additional two generations per year could be achieved under changing climate conditions

(Morimoto *et al*., 1998). A potential increased growth season may, however, be limited by the timing of resources, although if resources persist for longer in agricultural environments, it can generally be expected that the pest may, too. Indeed, crop yields may increase in vegetative crops due to the increased duration of suitable growing conditions. Cereal crops are unlikely to benefit from warming conditions; however, as the speed of development increases, the size of the grain is likely to reduce significantly, and therefore the overall yield (Gregory *et al*., 2009). The quality of these structures as a food source for insects is likely to decrease due to an increased carbon to nitrogen ratio in the plant tissues (Coviella and Trumble, 1999). This will require insects to increase their food intake in order to maintain function, impacting their metabolic rate and resulting in fitness costs. Greater vegetative damage may also increase the potential for pathogen infection of crop plants, either through direct transmission of viral pathogens or through opportunistic infections, further impacting the sustainability of crop practices (Gregory *et al*., 2009). These results appear to paint a bleak future for agriculture; however, in warmer climates, an increase in temperature will also place species closer to their upper thermal limits, perhaps effectively limiting population persistence, despite the potential for increased voltinism. The interplay between faster generation times, reduced performance windows and lower food quality indicates that predictions of agricultural pest damage may not be simple to make and are probably subject to change.

With faster developmental rates and generation times comes the potential for an increase in the speed of the adaptive process. This could be beneficial for allowing species to undergo evolutionary changes to remain within their current native range, or even potentially expand their distributions. There is also the potential to use physiological responses, either within or between life stages or generations, to buffer the immediate impacts of climate change until they can mount an adaptive response. Very few studies have measured the potential for adaptive and plastic change in physiological traits for ectotherms, particularly in light of a changing climate. What has been measured, however, indicates that there are latitudinal differences in the severity of climate change impacts and species ability to evolve in response to climate variation. In general, mid-latitude populations or species experience greater heat stress conditions at present, and this is predicted to increase over time (Hoffmann *et al*., 2013). There also tends to be more thermally specialized species that have evolved to operate maximally at lower latitudes, probably because of the reduced levels of thermal variation in comparison to higher-latitude environments. Current evidence suggests that these low-latitude tropical species exist in habitats that experience conditions close to their upper thermal limits, indicating that they have a lower 'warming tolerance' (WT), defined as the difference between current habitat temperature and thermal maxima for survival and performance (Deutsch *et al*., 2008). Comparisons of different insect species show that upper thermal limits are more constrained and tend to be more similar across closely-related species. This indicates that there may be some limits to evolution that persist across all groups (Hoffmann *et al*., 2013). Direct studies of adaptive potential, through selection experiments and heritability assays in *Drosophila*, indicate that the ability of insect species to mount an evolutionary response to increased upper thermal limits may, in fact, be limited (Mitchell and Hoffmann, 2010; Hoffmann *et al*., 2013). How these results apply to other insect species remains to be determined, but could significantly affect their ability to respond to long-term changes in environmental conditions.

To date, the majority of models used to predict species future distributions under climate change are unable to account for the ability of species to adapt (Pearson and Dawson, 2003). Evidence suggests that, at least for upper thermal limits, this may not necessarily be an issue (Addo-Bediako *et al*., 2000). However, the methods used to predict adaptive potential are limited to studies on model organisms or are estimated by proxy using association studies with current environmental conditions.

The most common projective models, climate envelope models (CEMs), also use current presence/absence data for populations and correlate environmental variables to characterize the environment where the species can survive and then use these descriptive variables (generally temperature and humidity estimates) with predicted changes in climate to project future distributions (Elith *et al*., 2006). These estimates typically do not include direct estimates of physiological limits or adaptations thereof and also cannot account for changes in abiotic and biotic factors that may limit species' distributions under novel conditions. They also tend to focus on very simple predictions of future environmental conditions, i.e. a steady increase in temperature coupled with reduced precipitation (Pearson and Dawson, 2003). For species for which we have little ecological and physiology data, these methods provide a useful proxy for understanding potential range shifts under changing climate conditions and can be used as a starting point to begin more detailed studies. Additional levels of complexity can then be added later to improve future projections. This can be achieved by the use of more mechanistic distribution models, where biotic information such as thermal tolerance limits can be used to train the model to identify environmental factors and then make more complex predictions of future range shifts and, in the case of agricultural pests, create pre-emptive strategies for dealing with potential invasion or changing pest status under climate change (Buckley *et al*., 2011).

In general, predictions for distributions and population dynamics of agricultural pest species indicate overall expansion or shifts of geographic limits towards higher latitudes or altitudes and a higher fecundity and shorter development time (and therefore increasing population sizes) under global climate change. Table 6.1 provides a brief example of the models utilized and the outcomes predicted for several key agricultural pests. To date, the majority of studies have modelled distribution using correlative model approaches, with very few utilizing physiological and phenological data to add

Table 6.1. Some examples of the predicted change in the range of different insect pest species due to climate change.

Species	Area	Model	Prediction	Reference
Western corn rootworm (*Diabrotica virgifera virgifera*)	Northern hemisphere	Multidimensional envelope modelling (MDE) or Mahalanobis distances (MD)	Northward movement of the physiological limits; increased outbreaks at higher altitudes	Aragón and Lobo, 2012
Codling moth (*Cydia palmonella*)	Norway	CLIMEX	Extension of geographical range, increase in abundance in established locations	Rafoss and Sæthre, 2003
Peach fruit fly (*Bactrocera zonata*)	Worldwide	CLIMEX 3.0 and GIS software	Expand towards the poles into colder regions	Ni *et al*., 2012
Coffee berry borer (*Hypothenemus hampei*)	East Africa	CLIMEX 3.0	Shift to higher altitudes; increase in number of generations per year	Jaramillo *et al*., 2011
European corn borer (*Ostrinia nubilalis*); Colorado potato beetle (*Leptinotarsa decemlineata*)	Central Europe	CLIMEX	Developmental limitations will shift; widening areas of occurrence, shift to higher altitudes, coupled with more generations per year species	Kocmánková *et al*., 2011

detail to their predictions. As it is known that including additional data may reduce the uncertainty in predictive models (e.g. Aragón and Lobo, 2012), this raised the question of whether the absence of mechanistic model estimates was due to insufficient physiological data for pest species. In order to investigate this possibility, we conducted a meta-analysis on current upper thermal tolerance estimates of insect pests. We also sought to explore what might happen under climate change, using the metrics available, such as warming tolerance.

A recent study by Hoffmann *et al*. (2013) compiled all known thermal tolerance estimates for insect species worldwide. Using Internet searches and the CABI® Crop Protection Compendium (www.cabi.org/cpc/), each species from this list was assessed to determine if it was defined as an agricultural pest, i.e. its food sources included species generally grown for agricultural harvest. Our final analysis focused only on the species listed in the Hoffmann *et al*. (2013) database, resulting in 15 species from the original approximately 380 species included in the analysis. As there were more species represented in upper versus lower thermal limits tables from Hoffmann *et al*. (2013; supplementary tables), we focused our analysis on the estimates of CT_{max} or ULT. Location data from each study included in our assessment were used to obtain current environmental data (i.e. mean maximum temperature, mean temperature in warmest quarter) for each species and compared to averaged future estimates of environment from three different models (CCCma, CSIRO mk3 and HadCM3) for 2030 and 2050 using the downscaled data from the Research Program on Climate Change, Agriculture and Food Security (CCAFS; http://www.ccafs-climate.org/data/). WT was calculated as the difference between species' estimated tolerance for CT_{max} or ULT and the predicted overall mean temperature or temperature in the warmest quarter averaged across the three models, and provided an indication of the thermal window between projected warming and the species' upper thermal limits. There were very few species for which there were data for both CT_{max} and ULT; therefore, analyses were conducted at the trait or life-stage level. We also examined the representation of upper thermal tolerance studies on pest species across the different biogeographic zones. In order to simplify the analysis, we grouped the agricultural pest species for which there was upper thermal limit data (both CT_{max} and ULT) by taxonomic family level and plotted the source locations of these studies (Plate 1), showing that there was strong biogeographic bias in where such information was collected.

All fifteen pest species showed a reduction in warming tolerance under future climate projections for both CT_{max} and ULT, and this was more obvious when examining mean temperature change rather than the mean of the warmest quarter (Fig. 6.3). This reduction was significant overall for the mean temperature change and was more pronounced in the egg and larval life stage than in adults (Mann-Whitney U test, $U = 304$, $p < 0.05$; Fig. 6.3). This would indicate that the earlier developmental stages might limit the overall persistence of pest species under warming conditions, albeit without taking into consideration microsite differences and potential behavioural buffering. There was a significant overlap of upper thermal limits, seen as points on the secondary *y*-axis (Fig. 6.3). This may indicate a restricted ability to adapt in these traits; however, this would need to be examined across a larger number of species. From the approximately 380 species represented in the Hoffmann *et al*. (2013) database for upper thermal limits, agricultural pests made up only 4%, highlighting a potential critical information gap in the current literature. Of these represented families, Tephritidae had the highest global coverage of studies. There was a high concentration of studies conducted in Western Europe, and the only studies conducted on thrips and Drosophilids were conducted in Asia (Plate 1). Generally, this suggests a need for further pest thermal tolerance and development studies from a wider range of locations and taxa.

In general, climate models used for predicting pest species distributions are unable

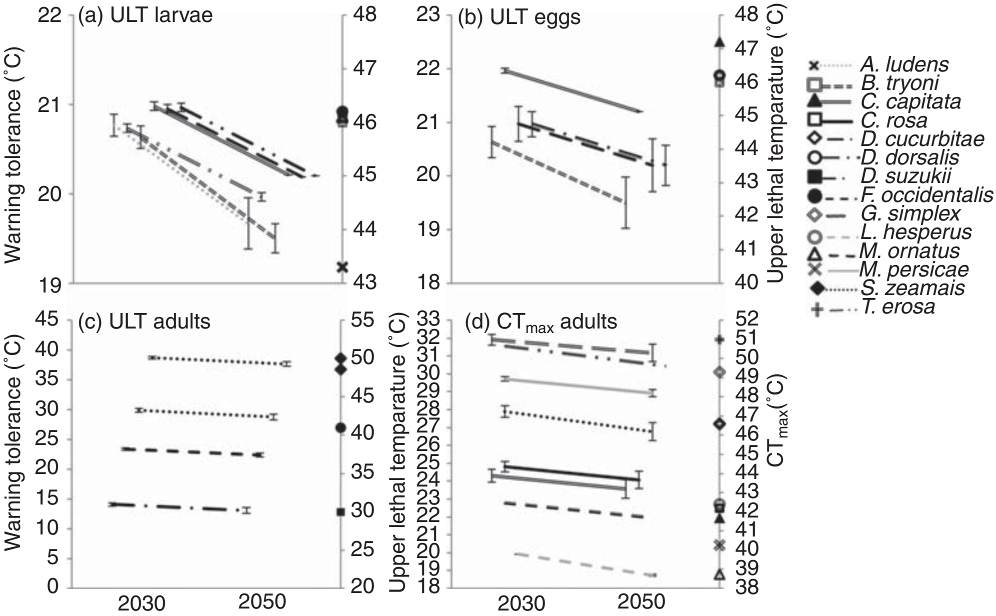

Fig. 6.3. Predicted impact of global climate change on upper thermal limits of agricultural pest species. Primary *y*-axis shows warming tolerance of each species, calculated as the difference between annual mean maximum temperature, as projected from climate scenario A1b, and the species estimated upper thermal limit (as upper lethal temperature, ULT, or critical thermal maximum, CT$_{max}$, depicted on the secondary *y*-axis). Climate data were the averaged future estimates from three different models (CCCma, CSIRO mk3 and HadCM3) for 2030 and 2050 and extracted from downscaled data from CCAFS (www.ccafs-climate.org/data). Each pattern represents one species, with multiple points of the same pattern depicting two populations of the same species (i.e. *S. zeamais* in panel (c)). (All species thermal limit data collated from Hoffmann *et al*., 2013, supplementary tables 2 and 3.)

to incorporate thermal physiology limits, due to a severe absence of published literature for agricultural pests. Evidence from analyses of current distributions indicates that insect pests have already shifted their ranges in response to climate change, with a general poleward trend found across a large number of species (Bebber *et al*., 2013). This information, together with our current analyses of warming tolerance in species for which there is currently data, indicates that the general prediction of benefits for pest species under global climate change may well be misrepresented. Although the predicted climate variables we used for our analyses were conservative, and the estimates of thermal tolerance were based on the assumption that there was no potential for adaptation in these traits, there was still significant information to be gleaned from incorporating such data into projections of agricultural pest distributions, and therefore estimates of crop damage potential, in a changing environment. Overall, an urgent shift to studies is required of thermal tolerance. There is particular need to focus more studies on Asia, considering that it is the region with the highest estimated losses due to insect pests than any other part of the world (Rosenzweig *et al*., 2001). There is also an alarmingly small focus on studies on the African subcontinent, despite fears of food security in this region. Whether pest species will also be capable of moving the large distances necessary to invade novel habitats and continue to track the changing environmental conditions over a longer timescale has also yet to be determined and incorporated into predictions of climate change.

6.4 Movement and Dispersal in Agricultural Landscapes

Throughout this section, we use the term ‘dispersal’ in its broad sense for both gene flow (movement of propagules between populations; these propagules can be seed or pollen in plants or individuals of any life stage in animals, e.g. Segelbacher *et al*., 2010) and movement for foraging and other routine movements (e.g. daily home range). Dispersal rate is highly variable between different populations of the same species and between different species (Koenig *et al*., 1996). One of the most important areas of ongoing research involves estimating maximum flight or dispersal distance as it impacts the damage caused by the insect pest, as well as their distribution and abundance in both space and time (see Table 1 in Mazzi and Dorn, 2012). An increase in air temperature may increase the flight period and therefore enable organisms ultimately to disperse over greater distances. For example, Cormont *et al*. (2011) showed that time spent flying and the net displacement increased in four different butterfly species as temperatures increased. Similarly, Chidawanyika and Terblanche (2011) showed an overall positive relationship between the number of individual codling moths caught in pheromone traps and ambient air temperature in the range 16–30°C. Assuming these traps represent an unbiased estimate of field activity, this may signal that global climate change can impact pest species distributions greatly by providing larger periods of suitable thermal conditions for flight, perhaps increasing dispersal distances or reducing the costs of dispersal per unit of time.

Studies of dispersal in pest species have, however, produced conflicting evidence for dispersal capacity, which may be due partly to variation in the methods used. The movement of individuals between populations can be measured using different approaches, including direct and indirect methods. Direct methods generally involve marking (e.g. fluorescent dust or stable isotopes), releasing and recapturing individuals under natural conditions or making use of radar (e.g. harmonic or vertical-looking radar) to estimate field fitness and performance, sometimes after subjecting groups to different treatments (e.g. Chidawanyika and Terblanche, 2011). These direct methods have been shown to have some limitations, as they may be biased due to spatially restricted sampling or additional dispersal events occurring during life stages that were not sampled (Bohonak, 1999). In contrast, indirect approaches, which typically make use of the genetic structure of a species, can be averaged over many generations (Bohonak, 1999) and are therefore more robust to these biases. Some studies have shown that estimates of gene flow employed using the indirect method can be compared to direct estimates of dispersal, but this is not true in all cases (Peterson and Denno, 1998; Bohonak, 1999). For example, in a flight mill experiment, Sharp and Chambers (1976) showed that *Ceratitis capitata* (Mediterranean fruit fly) had a maximum flight distance of 7–8 km. Similarly, in a mark-and-recapture trial, Meats and Smallridge (2007) showed that they could disperse 0.5–9.5 km (although most of the individuals remained within 400–700 m of the release point). By contrast, a recent population genetic structure study on *C. capitata* in South Africa (Karsten *et al*., 2013) showed that these flies dispersed to locations far more geographically distant than indicated by direct methods. If both methods are assumed to be reasonable indicators of movement, the latter study suggests a long-distance dispersal method is at play in *C. capitata* populations at a regional scale, and possibly is human mediated. The use of multiple estimation methods is, therefore, recommended in order to gain a better overall picture of the dispersal potential of pest species, particularly under global climate change.

If an organism has limited dispersal ability, this should decrease the amount of gene flow between different populations, which may lead to lower genetic diversity and higher levels of inbreeding (Suni and Gordon, 2010). The long-term persistence of populations is often dependent on gene flow to counteract population processes such as genetic drift and to maintain genetic variation (Segelbacher *et al*., 2010). Therefore, although climate change could allow for the extension of a pest species' range, it might not be possible to shift or establish in the new habitat due to this limited dispersal ability. Individuals that do disperse might also experience a trade-off with reproductive potential (e.g. Hughes *et al*., 2003), further decreasing the chances of establishing a population in a novel habitat. However, as a disproportionate amount of pest species can reproduce asexually (Hoffmann *et al*., 2008), the impact of such a trade-off may not be as significant.

The establishment of populations in new areas is commonly characterized by low population densities and repeated introductions (i.e. high propagule pressure). With expected change in climate, some species are predicted to have faster development times associated with warmer temperatures, and therefore an increased number of generations per year. This would allow both native and invasive species to overcome some of the barriers posed by small effective population sizes. Species introduced via human-mediated dispersal (jump dispersal) may be particularly favoured, as the probability of the failure of establishment due to unfavourable conditions is likely to decrease. Some potential support for this line of reasoning is provided by Meineke *et al*. (2013), who showed, for example, that increased temperature could be an important driver in the outbreak of pests on urban trees. They concluded that since the magnitude of change in both climate warming and urban warming was similar, their research could be used as a proxy to indicate outbreaks of pest species in agricultural landscapes. Similarly, expected regional changes in precipitation due to climate change will likely influence insects in different ways, although in many agricultural landscapes, artificial irrigation modifies the abiotic environment significantly, and perhaps also the pest's population dynamics.

6.4.1 Connectivity of the agricultural landscape

In the past few decades, there has been an intensification of agricultural production, with the conversion of natural habitat to a managed, simplified, homogeneous landscape (Tscharntke *et al*., 2005). Zabel and Tscharntke (1998) showed that small-scale habitat fragmentation caused a decrease in the abundance and diversity of insects associated with stinging nettle. Such landscape modification often results in isolated patches of habitat (fragmentation), which in turn influences the effectiveness of dispersal between populations. This, in combination with a change in climate, can cause the habitat of the pest species to shift, degrade or improve. These effects are typically seen more readily at the edges of species or population ranges (Sexton *et al*., 2009); however, for species with metapopulation structure, the stability of all connected populations may be affected adversely by this disturbance (Thomas and Hanski, 2004). Evidence to date cautions against the ongoing transformation of the landscape, which is predicted to favour pest species greatly in the future (Mazzi and Dorn, 2012). As species differ in their ability to cope with disturbance, and also to disperse, a change in landscape structure will alter the actual connectivity of the landscape differently for each organism (Mazzi and Dorn, 2012). Estimating the dispersal distance (Table 6.2, redrawn from Table 1 in Mazzi and Dorn, 2012) of a pest species is therefore a requirement for a successful area-wide pest management strategy, and is of increasing importance. The patterns of gene flow, as well as the genetic variation between different pest populations, can demonstrate the state of the available habitat (Roderick, 1996), as well as the potential for evolutionary change.

6.4.2 Dispersal and biological control

Dispersal in the agricultural landscape also plays a key role in the effectiveness of pest

Table 6.2. Selected estimates of average short-range dispersal distances from mark–recapture studies in food crops published within the past 10 years.[a] (Redrawn from Mazzi and Dorn, 2012, Table 1.)

Order, species (family)	Host crop	Gender	Distance (m)	Recapture method	No. released/recapture rate (%)	Reference
Lepidoptera						
Southwestern corn borer (*Diatraea grandiosella* (Crambidae))	Maize (*Bt*)	Males	93–97	Light traps and pheromone lures	1894/2–18	Qureshi *et al.*, 2006
European corn borer (*Ostrinia nubilalis* (Crambidae))	Maize	Females	94	Light traps	1276/0–4	Engels *et al.*, 2008
		Pooled	195	Light traps	736/10	
European corn borer (*O. nubilalis* (Crambidae))	Maize (*Bt*)	Males	96–183	Light traps and pheromone lures	13,942/3–10	Qureshi *et al.*, 2005
		Females	93–96	Light traps	9977/0–4	
Potato moth (*Phthorimaea operculella* (Gelechiidae))	Potato	Males	76–255[b]	Pheromone lures	12,000/2	Cameron *et al.*, 2002
Diamondback moth (*Plutella xylostella* (Plutellidae))	Cauliflower and broccoli	Males	14–35	Sticky buckets and pheromone lures	11,000–33,000/3–19	Mo *et al.*, 2003
		Females	13–24	Sticky buckets	6000–18,000/14–19	
Codling moth (*Cydia pomonella* (Tortricidae))	Apple	Pooled	282	Pheromone and kairomone mixture lures	n.a. (self-marking)	Basoalto *et al.*, 2010
Codling moth (*C. pomonella* (Tortricidae))	Apple	Males	114–134[c]	Pheromone lures	1028/33	Keil *et al.*, 2001
Grape berry moth (*Endopiza viteana* (Tortricidae))	Grape	Males	13	Sticky pane traps and pheromone lures	*c.*1300/1–32	Botero-Garcés and Isaacs, 2004
			4	Sticky pane traps	*c.*1300/0–3	

continued

Table 6.2. *continued.*

Order, species (family)	Host crop	Gender	Distance (m)	Recapture method	No. released/recapture rate (%)	Reference
Coleoptera						
Sweet potato weevil (*Cylas formicarius elegantulus* (Brentidae))	Sweet potato and sugarcane	Males	237–318	Pheromone lures	13,916/14	Kumano *et al.*, 2007
Plum curculio (*Conotrachelus nenuphar* (Curculionidae))	Stone and pome fruits	Pooled	8–12	Sticky trunk screens and limb tapping	2100/19–23	Leskey and Wright, 2007
Sugarcane click beetle (*Melanotus okinawensis* (Elateridae))	Sugarcane and tobacco	Males	274	Pheromone lures	300/8	Arakaki *et al.*, 2010
Diptera						
Queensland fruit fly (*Bactrocera tryoni* (Tephritidae))	Stone fruits	Pooled	120	Sticky spheres and cue lures	81,300/1 (sticky); 13–18 (pheromone)	Meats and Edgerton, 2008
Mediterranean fruit fly (*Ceratitis capitata* (Tephritidae))	Mango	Pooled	*c.*20	Food baits	386/26	Epsky *et al.*, 2010
Hemiptera						
Glassy-winged sharpshooter (*Homalodisca vitripennis* (Cicadellidae))	Orange	Pooled	31	Sticky sheets	*c.*83,000/2	Blackmer *et al.*, 2006
Aster leafhopper (*Macrosteles quadrilineatus* (Cicadellidae)	Lettuce, endive, escarole, onion	Pooled	54	Vacuum sampling	*c.*93,000/0.2	Zhou *et al.*, 2003

Notes: Bt, Bacillus thuringiensis; n.a., not available; nr., number of individuals realeased. [a]Data for nonmanipulated controls are given whenever the original study compared treatment groups. Ranges are given whenever data from multiple realeases are reported in the original study, rather than averaged across replicates. Within orders, entries are sorted alphabetically, first by family, then by scientific species name and first author's surname; [b]Lower and upper estimates under the assumption of linear and radial dispersal, respectively; [c]Lower and upper estimates for artificially selected sedentary and mobile strains, respectively.

control, particularly through the use of biological control agents and the SIT. Due to the negative impact of pesticides and insecticides on human health and the environment, environmentally friendly techniques of insect control are preferred. The SIT is a commonly applied technique for insect population control worldwide. Although the SIT has been shown to be successful for some insects, including tsetse flies (Diptera: *Glossina* spp.) and screwworms fly (Diptera: *Cochliomyia*), other taxa have proved more challenging to control using this method. To be effective, some *a priori* knowledge is required regarding the population structure, movement patterns and spatial network of population connections. Moreover, identification of sites from which reinvasion is most likely to occur, and knowledge regarding the primary routes through which pests are likely to re-establish, are critical aspects of an area-wide management plan. To this end, determining gene flow among populations can help ensure that population control measures are successful and that pest control resources (e.g. baiting stations) are allocated efficiently. Understanding the factors that influence dispersal ability in natural populations may also aid in improving the ability of the released sterile insects to penetrate the local environment and expand their impact by decreasing the population sizes of pest species.

When the release of sterile individuals of the same pest species is not tenable (or the development of such an approach is still in its infancy), suitable biological control agents, i.e. predators or disease vectors of the pest species, can be released to decrease population sizes. However, previous studies have shown there may be a wide range of adverse effects, sometimes leading to these agents becoming invasive non-target pests. One such example is the seven-spotted ladybeetle (*Coccinella septempunctata*), which was released in the USA multiple times for the biological control of aphids (Angalet *et al*., 1979) and has since spread and become established, displacing native species in some of the newly invaded sites (Evans, 2004). This displacement forces the beneficial native species into surrounding vegetation due to a lack of resources, only allowing them to return when the aphid species (the original biocontrol target) reach sufficient numbers (Evans, 2004). This shift in population dynamics may further enhance the homogeneity of agricultural systems and effectively increases the dispersal cost to the native species, forcing them to move further in order to maintain their population sizes. Another example is that of *Cactoblastis cactorum*, the cactus moth, introduced from its native range in South America into multiple locations, including South Africa and Australia, for the control of prickly pear (*Opuntia cacti*) (Zimmermann *et al*., 2001). About 20 years ago, the cactus moth was discovered in North America, where it now threatens the native *Opuntia* used for food and fodder (Zimmermann *et al*., 2001).

The geographic range of insect pests in the agricultural landscape will likely be influenced by climate change in different ways. The capacity of an insect pest to adapt or move with the change in climate will be determined by its basal tolerances, behavioural and physiological opportunities for responses at shorter timescales, evolutionary potential at longer timescales and dispersal capacity. It is therefore increasingly urgent that dispersal, gene flow and evolutionary potential be investigated under a range of climate conditions in order to prepare management plans that account for such factors and thereby reduce uncertainty for future pest outbreaks and vulnerability to changing pest status.

6.5 Interactions Between Hosts and Biocontrol Agents and Potential Interactions with Climate

As mentioned previously, in the agricultural landscape, pest control can be achieved by the use of biological control agents, parasitoids or predators. Particular attention has been given to the interaction between pest populations and parasitoids, with environmental temperature proven to have a crucial role in mediating the outcome of host–parasitoid interactions (Geden, 1997;

Sigsgaard, 2000; Mironidis and Savopoulou-Soultani, 2009; Wang *et al*., 2012). Indeed, because both partners are ectotherms with certain specific phylogenetic (and ecological) proximity and an intimate relationship, host–parasitoid couples constitute suitable models for use in the experimental study of direct and indirect effects of temperature.

Host and parasitoid might be divergent in their thermal preferences, with both partners having their own unique thermal performance curve. If these performance curves overlap, no effects of temperature would be expected, but if their performance curves show some form of separation, the course of infection, or interactions more generally, could be influenced strongly by temperature variation (Thomas and Blanford, 2003; see also Vucic-Pestic *et al*., 2011, on predator–prey interaction rates). For instance, Wang *et al*. (2012) demonstrated slight but significant differences in the thermal performances among a California population of the olive fruit fly, *Bactrocera oleae* (Diptera: Tephritidae), and African populations of two parasitoid species, with implications for predicting the establishment of candidate parasitoids in the host's invaded habitat.

A number of studies have also now demonstrated that host susceptibility and disease virulence are temperature dependent (Blumberg, 1991; Thomas and Blanford, 2003; Hance *et al*., 2007). For example, the encapsulation ability of *D. melanogaster* lines that had been selected for increased defence to different larval parasitoid species and measured at a variety of temperatures shows specific patterns according to the host–parasitoid combination (Fellowes *et al*., 1999).

However, to be able to make predictions on the effects of climate change on the outcome of host–parasitoid interactions, it is necessary to have more realistic studies than those realized on only one host population and under constant controlled temperatures. To achieve such a goal, a few studies have started to address the effect of fluctuating temperatures (Awadalla, 1996; Geden, 1997; Bahar *et al*., 2012; Foray *et al*., 2013), or to take into consideration the interaction of the between-population variability of host and parasitoid species. Recently, Bahar *et al*. (2012) demonstrated significant differences between constant and fluctuating temperature regimes on most parameters of the development of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), and its North American parasitoid, *Diadegma insulare* (Hymenoptera: Ichneumonidae). Ris *et al*. (2004) showed, by investigating the development of two lines of the parasitoid, *Leptopilina heterotoma* (Hymenoptera: Figitidae), on a different combination of hosts (three different *Drosophila* species) and temperatures (four developmental temperatures), that both host and temperature interacted strongly to shape the parasitoid phenotype and that complex genotype-by-environment interactions could even invert the relative fitness of the two parasitoid lines. To our knowledge, only one study has considered both fluctuating temperature and the genetic variability of the host, but on a host–fungi interaction. By using different clones of the pea aphid, *Acyrthosiphon pisum* (Hemiptera: Aphididae), and its fungal pathogen, *Erynia neoaphidis*, Blanford *et al*. (2003) showed that aphid susceptibility varied with temperature (constant or fluctuating regimes), with all clones showing some level of resistance under certain conditions but with the rank order of clonal resistance differing across thermal regimes.

Understanding complex interactions between host genetic variability and temperature fluctuations is absolutely necessary to be able to predict the effect of climate change on the ability of biocontrol agents to regulate pest species.

Péré *et al*. (2013) assessed how global warming would affect insect parasitoids and their role as natural enemies of insect pests by carrying out a meta-analysis based on 32 publications that used elevational gradients as analogues for global warming. Their study showed that both parasitism rates and parasitoid richness decreased significantly with increasing elevation, especially for endoparasitoids, suggesting an increase in parasitism with increasing temperature. Even if the results are interpreted cautiously because of possible bias (e.g. the fact that in most cases host density was unknown), this kind of study is informative and should be developed in the future.

6.6 Summary and Conclusions

Despite a strong focus for more than a century on environmental physiology for a number of charismatic pest species, this chapter has emphasized that insect pest responses to climate change are generally understood rather poorly, especially under field conditions where much work to date has been generally correlative in nature. However, on a rather positive note, several principles that have been developed for understanding an insect's environmental physiology more generally appear to transfer well to help forecast an insect pest's responses to climate change (e.g. increased risk of overheating, warming tolerance). On the other hand, this chapter has highlighted the biogeographic skew (or bias) in physiological knowledge of the effects of even a single, major abiotic factor such as temperature. Clearly, further work is required to monitor responses and changes in demography (e.g. phenology) with climate change for key pests, and further attempts to understand how climate change impacts other variables in the agricultural landscape that may mediate or amplify changes in demographics with climate change (e.g. dispersal) would be valuable. Also apparent from this review is that further integration between large-scale circulation models of climate change and fine-scale crop resolution, in order to predict, for example, insect body temperature, are essential avenues for research development. It would, furthermore, be extremely advantageous to develop high-throughput, remote methods of estimating insect body temperature under field conditions (e.g. molecular telemetry). Currently, coarse-resolution climate data present a significant challenge to forecasting insect responses to climate change in agricultural landscapes, especially at the scale of the individual organism (see discussion in Potter *et al*., 2013). Moreover, it remains generally unclear whether crop damage, or even simply pest abundance, will increase with climate change, or whether increases in some rates (e.g. growth) will be balanced by reductions in others (e.g. mortality, dispersal). Further work on this pressing topic, integrating a range of approaches and disciplines, is clearly essential for sustainable agriculture in a changing world.

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7

Climate Change and Biological Control in Agricultural Systems: Principles and Examples from North America

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Abstract

Biological control of pests is a key feature of integrated pest management programmes in many agroecosystems. An assessment of the potential impacts of climate change on biological control is critical but challenging, because biological control depends on interspecific interactions, which are generally complex. This chapter considers the potential effects of projected climate change on the biological control of insect pests, focusing on North American agricultural systems but involving principles that apply globally. The drivers of importance are projected rising surface temperatures, increased atmospheric CO_2 concentrations and changes in the amount of and variability in precipitation. We consider how these climate change drivers could affect biological control by: (i) directly affecting the physiology or behaviour of biological control agents and/or pests; (ii) changing the overlap between species in space and time; and (iii) modifying interactions among multiple species involved in biological control within the agroecosystem. We illustrate with the few North American documented examples of the sensitivity of biological control to climate change, or with data that indicate such sensitivities exist. Effects of the first type include increases in the occurrence of temperatures that exceed the thermal optima of natural enemies, such as those that have been documented for coccinellids. Effects of the second type include changes in phenological overlap between insect pests and their natural enemies, illustrated best by a recent report involving the cereal leaf beetle and its principal parasitoid. Effects of the third type include climate-related changes in plant responses to herbivory that influence natural enemies, to the effects of climate on interacting predator assemblages and food webs. Although there is evidence for each of these types of effects, the literature remains sparse. More studies are needed, and we suggest a research agenda to improve understanding of the sensitivity of biological control to climate change.

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Climate Change and Insect Pests
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7.1 Introduction

Climate change is expected to affect agricultural production worldwide, but with differing severity among agriculture systems and regions (Easterling *et al*., 2007; Porter *et al*., 2014). The responses of agricultural systems are difficult to predict because of their complexity (Sutherst *et al*., 2007; Staudinger *et al*., 2013). The biological control of insect pests exemplifies this complexity because it relies on the outcomes of the interactions of multiple species. In this chapter, we consider the potential effects of projected climate change on the biological control of insect pests in North American agricultural systems, although the principles discussed here apply globally (e.g. Thomson *et al*., 2010). We consider how climate change could affect biological control by: (i) directly affecting the physiology or behaviour of biological control agents and/or pests; (ii) changing the overlap between species in space and time; and (iii) by modifying interactions among multiple species within the agroecosystem involved in biological control. These mechanisms are hierarchical or interdependent (Fig. 7.1). We identify gaps in research needed to anticipate shifts in agricultural practices that might mitigate the harmful effects of climate change on biological control, including a consideration of the effects of evolution on these interactions.

The factors most likely to impact the resilience and adaptability of agroecosystems are: (i) rising surface temperature; (ii) increased atmospheric CO_2 concentration; (iii) variability in precipitation; and (iv) the interactions among these factors. All of these aspects of climate have changed significantly in North America and are projected to continue changing (Walsh *et al*., 2014). Mean annual temperatures increased significantly in the USA from 1901 to 2006, with regional trends ranging from –1 to >+2°C (Walthall *et al*., 2012). These temperatures are projected to increase by an additional 1.0–1.5°C by 2050, with greater increases at mid-latitude coastal regions and northern latitudes (Christensen *et al*., 2007). Similarly, global atmospheric CO_2 concentration, currently 390 ppm, is projected to reach 500–900 ppm by the end of the 21st century, due to anthropogenic emissions (Nakicenovic and Swart, 2000). Shifts in total precipitation and seasonal

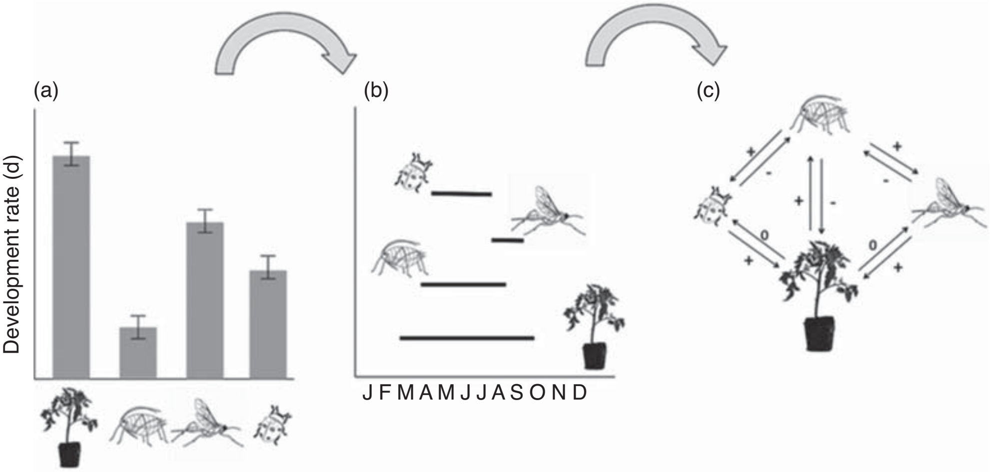

Fig. 7.1. The effects of climate change on biological control have a hierarchical structure. For example, rising average surface temperatures can be expected to impact aspects of insect physiology such as development rate (a). These impacts translate into phenological shifts (b), which ultimately affect the strength and direction of the tritrophic interactions (c) on which biological control relies. Thus, exogenous drivers that alter the processes in (a) are likely to scale up to alter the processes at the levels of (b) and (c).

patterns have been and are projected to be variable, depending on the region and latitude, changes in total precipitation and seasonal patterns (Walsh *et al*., 2014).

Collectively, the impacts of all three factors stand to alter the delicately balanced ecology of biological control. Successful biological control depends fundamentally on the viability of natural enemy populations and the per capita ability of these natural enemies to locate, subdue and process prey. Climate change will potentially directly affect the physiology and behaviour of natural enemy and prey, altering the effectiveness of biological control. Of the three projected trends for North American climate, warming may have the greatest potential direct effect on biological control through direct effects on predator and prey biology, ranges and phenologies. The effects of elevated CO_2 are expected to stem primarily from bottom-up influences of altered plant chemistry on herbivores, which may cascade to higher trophic levels (see section below). Changes in precipitation are difficult to assess in general terms because trends and projections are less certain and variable. Variability alone may affect biological control; for example, a meta-analysis detected a negative relationship between variability in precipitation and per cent of parasitism of caterpillars in forest systems (Stireman *et al*., 2005). The causes of this pattern are unknown, and its relevance for agricultural systems is uncertain.

7.2 Direct Effects of Climate Change on Pests and Natural Enemies

Warming climates potentially exceed the thermal ranges or thermal optima of natural enemies in some parts of their existing range, or permit species establishment where they are currently excluded by cold temperatures or extremes. Among generalist predators, ladybird beetles (Coleoptera: Coccinellidae), important aphid predators worldwide (Obrycki and Kring, 1998), have been well studied for their thermal ecology (Obrycki and Tauber, 1983; Honěk and Kocourek, 1988; Frazer and McGregor, 1992; Lamana and Miller, 1998; Rodriguez-Saona and Miller, 1999). Lower developmental thresholds for North American species, or those that have been introduced into North America, range from 7 to 12°C (Honěk and Kocourek, 1988), with implications for their sensitivity to warming. For example, the harlequin ladybird beetle, *Harmonia axyridis* Pallas, has been intentionally and unintentionally released in the USA on numerous occasions for the control of aphid species (Obrycki and Kring, 1998; Koch, 2003), but its northward range expansion into eastern Canada is evidently limited by its tolerance to cold temperatures. In five experiments, *H. axyridis* adult survival was 0% over winter in Quebec, Canada (Labrie *et al*., 2008). A warming climate could facilitate the northward expansion of this predator and others with low cold tolerance. The climate envelope of coccinellids is also constrained by high temperatures, since their development tends to decline in regimes above 30°C. For example, the larvae of *H. axyridis* reared under warm (>33°C) temperatures produce smaller adults than larvae reared under cooler temperatures (20°C) (Koch, 2003; Knapp and Nedvěd, 2013). This should reduce beetle fecundity since body mass is generally positively correlated with fecundity in insects, including coccinellids (Honěk, 1993; Davis and Landolt, 2012). Thus, projected warming could reduce populations of *H. axyridis* and *Coleomegilla maculata*, undermining the capacity of these species to suppress aphid populations. The thermal requirements of other insect predators have been less studied than those of Coccinellidae. Honěk and Kocourek (1988) have included summarized data for North American Chrysopidae and Hemirobiidae and reported intra- and interspecific variation in lower developmental thresholds, but there are no studies documenting upper thermal limits of these predators.

The impact of warming on biological control depends on the responses of prey and natural enemies. However, where the thermal developmental thresholds of coexisting predator and prey are similar, warming may cause similar range shifts or responses to climate by both species without affecting biological control. For example, the coccinellid, *Stethorus punctillum* Weise, and its prey, *Tetranychus mcdanieli* McGregor (Acarina: Tetranychidae), both important in raspberry systems in Quebec, have similar thresholds and temperature ranges for development (Roy *et al*., 2002). Development for the predator occurs from 14 to 34°C, while that for the mite occurs from 14 to 36°C; models for developmental thresholds indicate potential synchrony between these species. Lower and upper temperature thresholds have been established for several aphid species (Hazell *et al*., 2010a,b) and appear similar to those of the coccinellids that have been studied. None the less, small differences in the thermal ranges of natural enemy and prey, coupled with warming, potentially release the prey from biological control. Thermal mismatches occur for some parasitoids of lepidopteran pests in North America. The thermal maximum for *Plutella xylostella* L. (Lepidoptera: Plutellidae) is as high as 35°C, which is higher than that for one of its exotic parasitoids (Shirai, 2000) and for its North American parasitoid, *Diadegma insulare* Hellen. Pupal mortality of *D. insulare* increased with increasing temperature regimes from 7°C to 30°C, while pupal mortality for the caterpillar was unchanged at all tested temperatures (Bahar *et al*., 2012). The parasitic wasp, *Cotesia marginiventris* Cresson (Hymenoptera: Braconidae), failed to complete development in its host, *Spodoptera exigua* Hubner (Lepidoptera: Noctuidae) at 33°C, but developed successfully at 26°C, suggesting that warming could interfere with biological control by this relatively generalized species in western USA (Butler and Trumble, 2010). The climatic conditions required for stable host parasitoid dynamics have been developed theoretically for forest systems, with instability associated with different thermal bases for host and parasitoid (Hance *et al*., 2007). Similar effects may occur for parasitoids of crop pests, but no study has examined this.

In addition to directly affecting natural enemy physiology, warming potentially affects the behaviour of insect predators and parasitoids. Prey consumption depends on the functional response (per capita prey consumption rate as a function of prey density), which exhibits a hump-shaped response to temperature, rising to a maximum and then declining (based on a meta-analysis of records, including records from North America) (Englund *et al*., 2011). The maxima for prey attack and intake rates were near 24°C and 26°C, respectively, suggesting sustained average temperatures above these values might begin to erode biological control. This hump-shaped response of the functional response to temperature was confirmed experimentally for *C. maculata* (Sentis *et al*., 2012). Logan *et al*. (2006) modelled the effects of temperature on the predation of grasshoppers by spiders (Lycosidae) and included a handling time component that varied based on known temperature-dependent activity of spiders and grasshoppers. This model indicated that with increasing daily average June temperature (from 15 to 21°C) in western Nebraska, relative impacts of spider predation decreased and became negligible, due partly to the time available for prey searching. These studies indicate a relatively robust effect of warming reducing per capita prey consumption by generalist predators.

Temperature regimes also can affect foraging behaviour at the landscape scale. For example, dispersal by *H. axyridis* in the Midwestern USA (Ohio) is determined primarily by air temperature, rather than photoperiod. Huelsman *et al*. (2002) found that migratory flight activity generally took place on the first days exceeding 18°C after freezing temperatures. If temperatures warm significantly earlier than the historical norm, this temperature threshold may be reached, and beetles could begin migrating prior to aphid migratory flights, which also rely strongly on photoperiod (Blackman, 1971; Dixon, 1977).

7.3 Climate Change Effects on Species Overlap in Space and Time

Phenological shifts and range expansions are among the best-documented effects of warming trends on insect species (Parmesan and Yohe, 2003). If these shifts occur unevenly among interacting species, the temporal or spatial synchrony of biological control can be disrupted (Harrington *et al*., 1999; Bale *et al*., 2002; Both *et al*., 2009). Pests that extend their range beyond those of their principal natural enemies potentially escape biological control. Although this is a concern in North American agriculture, there are currently no published studies documenting such an effect.

Mismatches in phenology also potentially undermine biological control, which depends on the temporal co-occurrence of the vulnerable stages of the pest and the attacking stage of the natural enemy. Phenological mismatches can arise if interacting species respond to different environmental cues, including thermal units, precipitation, soil moisture, day length and other factors that will vary due to climate change. Indeed, within an ecological community, diverse responses to changing climates are the expectation (Durant *et al*., 2007), even within a functional guild. For example, Visser and Both (2005) reviewed 11 studies in terrestrial systems and found that climate-driven changes in the phenology of consumers frequently caused some misalignment with the availability of food resources, suggesting that mismatches of this sort might be common.

Although classical biological control depends on phenological alignment, in which the foraging stage of the agent coincides with the vulnerable stages of the target pest, overlaps can be imperfect, for various reasons, even under current climatic conditions. A well-documented example in a North American forest system illustrates this principle. The parasitoid, *Apanteles melanoscelus* Ratzeburg (Hymenoptera: Braconidae), was imported into North America to control the Gypsy moth, *Lymantria dispar dispar* L. (Lepidoptera: Lymantriidae). Field observations and laboratory experiments showed that the cool climate in the introduced range delayed parasitoid emergence relative to the host, forcing it to attack later instar caterpillars, which it parasitized ineffectively (Weseloh, 1975). None the less, phenological alignment can vary substantially interannually and spatially without disrupting parasitism, and possibly even helping to stabilize it (e.g. van Nouhuys and Lei, 2004). As climates change, however, biological control could be undermined by sufficiently large phenological misalignments. Evans *et al*. (2012) provide evidence that the phenology of the cereal leaf beetle (CLB), *Oulema melanopus* L. (Coleoptera: Chrysomelidae), and the introduced specialist parasitoid wasp, *Tetrastichus julis* Walker (Hymenoptera: Eulophidae), become misaligned during warmer springs in Cache Valley, Utah. Based on 10 years of field data, they found that the accumulated degree-days required by the beetle to reach the larval stages vulnerable to parasitism increased with the relative warmth of spring temperatures (to 1 June). In contrast, the degree-day requirements for parasitoid emergence were unaltered by spring temperatures. This resulted in poorer phenological matching and severely reduced parasitism during warm springs (Fig. 7.2). Evans *et al*. (2012) suggest that the mismatch arises because the overwintering adult beetles actively acquire thermal units in the spring, after emerging from diapause, by basking or otherwise seeking warmer microclimates, a strategy unavailable to the parasitoid, which at that time is completing development in puparia in the soil. If warm springs become more common, as is projected for the north-west USA (spring's >320 degree-days, base 9°C by 1 June, should increase from 0.1/year to >0.8/year by mid-century; Eigenbrode *et al*., unpublished data), phenological mismatches will disrupt biological control of *O. melanopus* in the region. The variable phenological overlap among years in this system evidently results from the differing capacity of the host and parasitoid to regulate their body temperature, and thus their metabolic and developmental rates. Thermoregulation is a well-known phenomenon in insects (Heinrich, 1993) and is responsible for phenological mismatches in one non-agricultural host parasitoid system (van Nouhuys and Lei, 2004). Phenological mismatches could arise through this mechanism in other biological

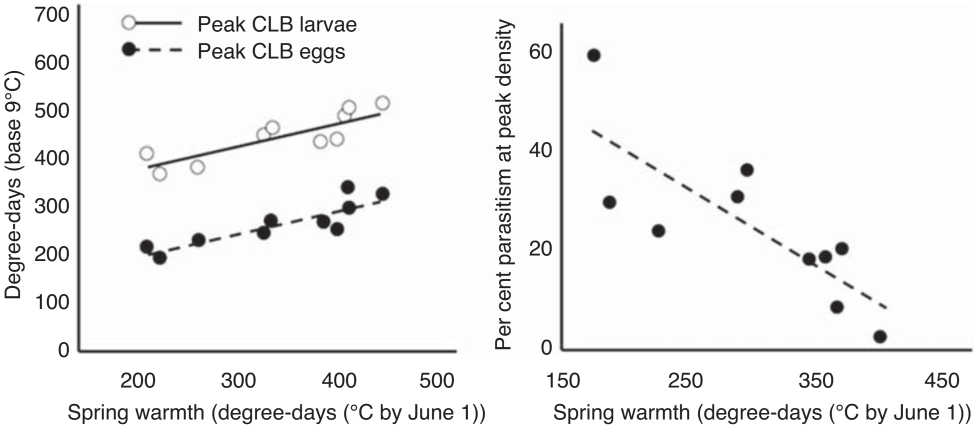

Fig. 7.2. Effects of warm springs on the phenology of the cereal leaf beetle, *Oulema melanopus*, and per cent parasitism by the specialist parasitoid, *Terastichus julis*. Left panel: degree-days (base 9°C) required for peak oviposition and peak larvae of *O. melanopus* in the Cache Valley, Utah, as a function of degree-days accumulated by 1 June during a 10-year period. Right panel: per cent parasitism of *O. melanopus* by *T. julis* as a function of degree-days accumulated by 1 June during a 10-year period. (Redrawn from Evans *et al*., 2012.)

control systems in agriculture under climate change.

Similar to classical biological control, conservation biological control depends on adequate synchrony of target pest and natural enemies. For example, predators and parasitoids vary in their phenological synchrony with their aphid prey in Brassica crops in British Columbia, which can compromise biological control (Prasad *et al*., 2009). Some specialist natural enemies within a naturally occurring complex have narrow phenological windows that can cause variation in their effectiveness among years (e.g. the 1-week active period of *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae), a parasitoid of aphids in spring cereals in the Pacific Northwest; Bosque-Pérez *et al*., 2002). The net effect of these individual perturbations will determine how the natural enemy community respond to changing climate.

Although the studies detailed above explore how overlap between species might vary under predicted climate change scenarios, few have examined the direct or indirect effects of climate change on species interactions in communities (Gilman *et al*., 2010). Yet, these interactions are likely to influence the responses of species to climate change significantly in both space and time (Berggren *et al*., 2009). For example, climate envelope models that predict range shifts in species may often fail to predict future distributions of species because they fail to account for species interactions (Davis *et al*., 1998). Thus, to predict overlap in natural enemy and pest species in both space and time under future climate scenarios, we must first have an understanding of how species interactions might change. This is detailed in the following section.

7.4 Effects of Climate Change on Species Interactions

At the level of communities, climate change is expected to influence species interactions and community structure, both of which could affect biological control. Each of these issues has been developed to some extent in previous sections, but here we expand our scope to consider entire communities and interactions such as plant defensive responses to herbivores, predation and competition. We first focus on how climate change is expected to mediate species interactions and present theoretical and empirical evidence of these effects. We then discuss how climate change can mediate community structure and the resulting impacts on biological control.

7.4.1 Effects on plant–insect interactions

Projected climate change is likely to influence not only prey and natural enemies but also the host plant, with implications for tritrophic interactions and biological control (Gutierrez *et al*., 2008). For example, the tomato hornworm, *Manduca sexta* L. (Lepidoptera: Sphingidae), is a serious pest of cultivated tomato (*Solanum lycopersicon*) in North America and elsewhere, but in the south-eastern USA it can be suppressed by naturally occurring and artificially augmented populations of the predator, *Podisus maculiventris* Say (Hemiptera: Pentatomidae), the most common predatory bug in North America (De Clercq, 2008). The phenolic rutin and steroidal alkaloid α-tomatine present in tomato tissues slow the development of *M. sexta* and reduce the fitness of *P. maculiventris* that feed on these caterpillars. But these effects are temperature dependent; caterpillar growth is slowed by rutin at cool but not warm temperatures (Stamp, 1990), while *P. maculiventris* fitness is reduced when fed caterpillars that had ingested rutin at warm but not at cool temperatures (Stamp and Bowers, 1991; Traugott and Stamp, 1996). As a result, as temperatures rise, direct and indirect effects potentially release *M. sexta* populations from control by this predator in tomato fields. These experiments used thermal regimes that differed by 5°C, which was similar to the magnitude of thermal shift projected by Walthall *et al*. (2012) from 2050 to 2099 in North America.

Tritrophic interactions can also be affected by increasing CO_2 concentrations, which can alter plant growth rates and the allocation of plant resources to growth, defence, C:N ratios and types of chemical defence (Coviella and Trumble, 1999). For example, in cotton (*Gossypium herbaceum* L.), increasing CO_2 concentrations cause a corresponding elevation in concentrations of the phenolic aldehyde, gossypol, which has an antibiotic effect on the herbivorous cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) (Gao *et al*., 2008). This resulted in improved fitness for the aphidophagous coccinellid predator, *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae), feeding on the aphid, potentially improving biological control. In contrast, Dyer *et al*. (2013) showed that increased CO_2 and temperature weakened the biological control of armyworm caterpillars by parasitoids on lucerne plants. In this system, increases in CO_2 or temperature decreased the nutritional quality of the lucerne host plants and the development times of the armyworm caterpillars. As a result, the parasitoids were unable to complete development, causing local extinction of parasitoid populations and weakened biological control (Dyer *et al*., 2013).

Ecologists have suggested that influences of rising CO_2 concentrations on insect population dynamics, particularly for agricultural pests, are contingent on ecosystem macronutrient dynamics, which are critical for plant growth. In other words, fertilizer levels and CO_2 concentrations could have unpredictable, interactive effects on plant growth. Cereal aphids and their parasitoids represent one example where the effects of elevated CO_2 have been examined at multiple trophic levels and with variable nutrient dynamics. Hoover and Newman (2004) developed a mechanistic mathematical model, parameterized with field data, to simulate six aphid species under variable CO_2 concentrations, temperature and nitrogen (N) inputs. Increased nitrogen fertilization increased aphid abundance and elevated CO_2 reduced aphid abundance at all temperature and N regimes. Yet, elevated temperature (2°C increase) increased aphid abundance at low N but decreased it at high N. Parasitoids increased consistently with aphid populations, such that their net relative effect on aphid populations at the projected increased temperature and CO_2 regimes did not differ from ambient. In other words, these authors did not find a noticeable interaction between climatic factors and parasitism, and suggest that parasitoids do not need to be considered when seeking generalities about climate change and aphid pests in cereals. This conclusion comes with caveats because of the assumptions used in building the model. Furthermore, the diversity of the responses that have been observed for aphids on host plants exposed to elevated temperature and CO_2 leaves the possibility of diverse responses at the higher trophic level as well. The contrasting prospects for the biological control of aphids in the cereal aphid system and the cotton system underscore the importance of species-specific examples when considering the potential responses of biological control to projected changes in temperature and atmospheric CO_2 concentrations. The model of Hoover and Newman (2004) is generic and applicable to cereal systems globally, including North America, but this applicability will require validation. Currently, there is a general lack of empirical models regarding the effects of CO_2 enrichment on tritrophic interactions in North American agricultural systems, so it is difficult to draw broadly meaningful conclusions about future expectations.

Herbivore-induced plant volatiles (HIPV) are attractive to predators and parasitoids in many systems, and mediate aspects of plant defence (Kessler and Baldwin, 2001) and biological control (De Moraes *et al*., 1998). Induction of plant volatile signals is sensitive to ambient temperatures, with implications for signalling natural enemies under climate change (Yuan *et al*., 2009). For example, Gouinguene and Turlings (2002) found that herbivore-induced volatile emissions from maize (*Zea mays* L.) were substantially higher under elevated temperatures ranging from 22 to 37°C, with a maximum occurring at 27°C. They also demonstrated that the composition of volatiles shifted across temperatures, such that qualitatively different odour plumes could be produced under varying thermal regimes. Although Gouinguene and Turlings did not examine the implications of these shifts for parasitoid attraction in bioassay, the amount and composition of HIPV are known to be important for response by parasitoids foraging for caterpillars on maize (De Moraes *et al*., 1998). The potential effects of changing climate on HIPV, and in turn on the effectiveness of biological control, are severely understudied.

7.4.2 Effects on natural enemy communities

Predator–prey interactions in communities may be most affected by the dispersal of species between communities and the degree of specialization (Gilman *et al*., 2010). For example, natural enemy species that are capable of long-distance dispersal may expand their ranges more rapidly under future climate scenarios and play a larger role in biological control than species with limited dispersal capabilities. Similarly, specialist natural enemies such as many parasitoids are likely to be influenced disproportionately by climate change compared to generalists, due to a high degree of dependence on a single host (Gilman *et al*., 2010). Thus, we might expect natural enemy communities comprised of generalists to be less affected by climate change than communities comprised mainly of specialists. Yet, it is unclear if this will improve biological control given that pest specificity is a cornerstone of classical biological control.

Variation in predator–prey interactions could strengthen, weaken or have no impact on biological control during periods of climate change (Fig. 7.3). Gillespie *et al*. (2012) demonstrated that biological control of the green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae), was increased by two parasitoid species, *Aphidius matricariae* Haliday (Hymenoptera: Braconidae) and *Aphelinus abdominalis* Dalman (Hymenoptera: Aphelinidae), during extended heatwaves. In this system, parasitoids competed less under heatwave scenarios and acted more complementarily, strengthening the biological control of aphids. In addition, aphids formed fewer alates during periods of elevated temperature, reducing dispersal and probably allowing for more effective parasitism (Gillespie *et al*., 2012). Similarly, Chase (1996) showed that an experimental shading treatment to reduce temperature and radiation increased the biological control of a grasshopper, *Melanoplus sanguinipes* (Orthoptera: Acrididae), by a wolf spider, *Pardosa* spp. (Lycosidae), in Montana. When grasshopper prey were shaded in morning hours, they had a reduced time available for feeding and spiders were able to exert stronger top-down control, resulting in a trophic cascade. In control plots, grasshoppers compensated for predation by increasing per capita survival rates and food consumption, leading to neutral effects of biological control in terms of plant growth.

In contrast, several studies have demonstrated negative indirect effects of climate change on biological control, caused by variation in predator–prey interactions. For example, Barton and Schmitz (2009) examined the biological control of grasshoppers (*Melanoplus femurrubrum*) by two generalist spiders (*Phidippus rimator* (Salticidae) and *Pisaurina mira* (Pisauridae)) in an old field system in Connecticut. Under ambient conditions, both spiders occupied distinct habitats, with the sit-and-wait species (*P. mira*) feeding near the plant canopy, while the active hunting species (*P. rimator*) foraged along the basal portions of the plants. In this case, the spiders did not overlap in habitat use and both contributed to biological control of the grasshopper prey. However, when temperatures were increased in experimental mesocosms, the sit-and-wait spider moved away from the plant canopy to seek shelter from the warm temperatures that were highest near the top of plants. This led to increased overlap in microhabitat use between the two spiders, which resulted in intraguild predation and local extinction of one spider species. In this case, climate change increased competition and intraguild predation, releasing the herbivore from control (Barton and Schmitz, 2009).

7.4.3 Effects on community structure and food web interactions

Despite the vast literature on species interactions, few studies have examined how interactions within food webs might influence biological control during periods of climate change (de Sassi and Tylianakis, 2012; Tylianakis and Binzer, 2014). In one of the only studies to examine this issue, de Sassi and Tylianakis (2012) showed that higher temperatures and elevated nitrogen benefitted herbivores disproportionately compared with plants and parasitoids in a temperate food web. Rising herbivore numbers reduced per capita parasitism rates and led to a weakening of biological control. This study highlights the importance of understanding interactions within entire food webs during periods of climate change. If it were generally true that herbivores were able to respond more rapidly to climate change than their predators, we would expect increased pest outbreaks under future climate scenarios (de Sassi and Tylianakis, 2012). Another recent study shows how biological control can be disrupted through complex indirect effects of a climatic factor on interacting species. Reduced precipitation (drought) reduced the quality of lucerne plants for the pea aphid, *Acyrthosiphon pisum* (Harris), and the abundance of this species. Fewer pea aphids reduced recruitment of a coccinellid predator, *H. axyridis*, in drought treatments. As a result, a second aphid species, the spotted aphid, *Therioaphis maculata*, which was not affected by the changes in lucerne quality under drought, was released from predation (apparent competition) on drought-stressed lucerne, reaching densities three times higher than on controls (Barton and Ives, 2014). Thus, the effects of climate change can ramify through a system and affect biological control. These factors are likely to be influenced by evolutionary processes, which we review later in this section.

At a community level, it is clear that climate change has caused the extinction of many species, and more are threatened (Sala *et al*., 2000; Tylianakis *et al*., 2008). This is problematic because communities with greater numbers of natural enemy species promote biological control (Hooper *et al*., 2005; Cardinale *et al*., 2006; Griffin *et al*., 2013). For example, in a system of five predators and parasitoids (*Geocoris pallens*

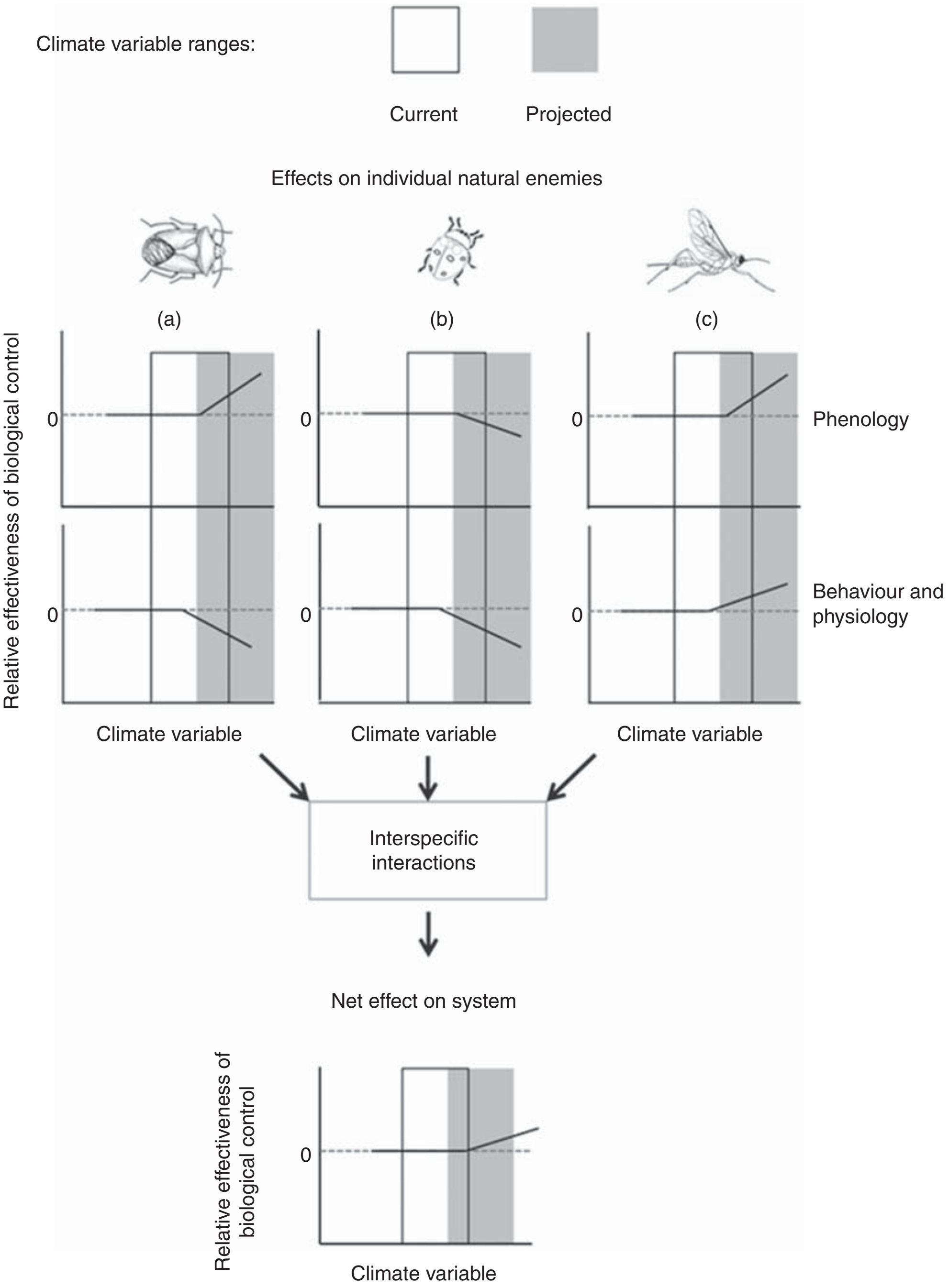

Fig. 7.3. Conceptual representation of the potential effects of climate change on biological control. Under projected climate change, the effectiveness of individual biological control agents will be affected through effects on their physiology and behaviour, geographic ranges and phenology. Depending on the species ((a)–(c) in this diagram), climate change might increase or decrease effectiveness (capacity to reduce pest density) via either type of mechanism. In this diagram, the *y*-axis represents relative change

continued

Stål (Hemiptera: Geocoridae), *Nabis* spp. (Hemiptera: Nabidae), *Coccinella septempunctata* (L.), *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) and *Diaeretiella rapae* (Mcintosh) (Hymenoptera: Aphidiidae)) feeding on cabbage (*Brevicoryne brassicae* L.) and green peach aphids (*M. persicae*), Snyder *et al*. (2006) showed that increasing richness of the natural enemy community increased biological control. These results were due to complementary interactions among the natural enemy species, such that each species provided some unique aspect of control (Gable *et al*., 2012). Similarly, Crowder *et al*. (2010) showed that more even communities of natural enemy species enhanced control of Colorado potato beetles (*Leptinotarsa decemlineata* Say; Coleoptera: Chrysomelidae). The enhanced control was attributed to reduced interspecific competition among natural enemies in communities that were not dominated by a single species. With reduced competition, the natural enemies were able to capture more effectively high numbers of prey. Since many studies suggest that higher trophic levels are most sensitive to climate change (Gilman *et al*., 2010), we might predict that negative impacts of climate change on biodiversity in natural enemy communities will continue to magnify over time, which could feed back to weaken biological control in many systems.

7.5 Future Research Needs and Conclusion

Projected climate change will affect biological control in agriculture through mechanisms from direct effects on the physiology and behaviour of natural enemies and prey species to more complex effects involving multispecies interactions (Fig. 7.1). Because of the diverse mechanisms, individualistic responses of natural enemies to climate and their interactions, the net effect of climate change on biological control in any system is uncertain (Fig. 7.3). Under projected climate change for North America, some key predators and parasitoids of crop plants will increase their ranges, or their ranges will shift, affecting spatial and phenological overlap with pests and their capacity to regulate prey populations. These mechanisms could either diminish or enhance the effectiveness of biological control in a particular system. Anticipating the effects of climate change on biological control in North America and elsewhere requires additional research because: (i) most systems are understudied or unstudied for the potential effects of climate change on biological control; (ii) existing studies are too few to draw robust generalizations; and (iii) the complexity of mechanisms and systems may preclude generalizations, requiring that most systems be studied individually. Research needs can be identified for each of the types of mechanisms around which this chapter has been organized.

7.5.1 Direct effects of climate change on pests and natural enemies

- Consider the effects of multiple climate drivers. Most research has focused on the effects of temperature, with fewer considering CO_2 or other drivers such as drought. More rare are studies that consider multiple climate drivers in combination, as they will occur under

Fig. 7.3. *continued*
in effectiveness, with zero representing effectiveness under the current climatic regime. The *x*-axis represents a range of some climatic variable under current and projected conditions. Each agent's relative effectiveness can be enhanced (e.g. species (b)) or diminished (e.g. species (c)) as a result of projected climate change. Furthermore, effects on phenology versus behaviour and physiology may differ for a given species (e.g. species (a)). Finally, these species interact among themselves and with others in the agroecological community to produce a net effect, which may be to enhance (as shown) or diminish the overall effectiveness of biological control.

climate projections (Hoover and Newman, 2004; Dyer *et al*., 2013).

- Incorporate variability in climate drivers. Experimental studies often employ fixed temperature regimes, but episodically fluctuating temperatures better mimic natural variability: those mimicking extreme events such as heat shocks may anticipate climate change impacts better. Studies that incorporate this variability are appearing (e.g. Harmon *et al*., 2009; Butler and Trumble, 2010; Bahar *et al*., 2012; Knapp and Nedvěd, 2013; Sentis *et al*., 2013), but more are needed.
- Include multiple stages of pest or natural enemy. The developmental stages of prey or natural enemies may differ in sensitivity or type of response to climate drivers (e.g. Knapp and Nedvěd, 2013). Where such effects are feasible, experimental designs should consider them.

7.5.2 Climate change effects on species overlap in space and time

- Identify long-term data sets for analysis. Detecting shifts in phenology and geographic range requires long-term data sets (e.g. Evans *et al*., 2012). Some existing data sets have not been fully exploited (e.g. Davis *et al*., 2014), or have not been organized to allow the detection of such shifts. Some of the data are unpublished or present in the 'grey' literature.
- Identify or start acquiring baseline data for longer-term data sets that can be used to detect and understand changes in biological control associated with climate change (e.g. Eigenbrode *et al*., in progress)
- Develop models driven by downscaled climate projections. Existing degree-day models and climate envelope models can be validated and coupled with improved climate projections to anticipate changes in phenological or geographic overlap (e.g. Olfert *et al*., 2004; Lozier and Mills, 2011).

7.5.3 Effects of climate change on species interactions

- Develop or adopt a theoretical framework. The conditions required for stable host–parasitoid dynamics have been developed theoretically for forest systems, with instability associated with different thermal bases for host and parasitoid (Hance *et al*., 2007). Similar regularities may occur for parasitoids of crop pests, especially perennial crops, but no study has examined this.
- Expand studies of the effects of climate change on chemical ecology. Yuan *et al*. (2009) make a coherent case for the potential effects of climate change, including warming, elevated CO_2, ozone and drought stress on chemical ecology involving plants and their associated ecological communities. The limited studies of the effect of temperature on HIPV (e.g. Gouinguene and Turlings, 2002) have detected effects on HIPV, but the implications for biological control have yet to be studied.
- Incorporate the effects of plant growth stage or tissue age in responses. Ballhorn *et al*. (2011) showed that leaf age in *Phaseolus lunatus* determined responses to CO_2, and in turn choice behaviour of a natural insect herbivore, the Mexican bean beetle (*Epilachna varivestis*). This suggests that higher-order interactions might also be affected by the developmental stage of the host plant.

7.5.4 Potential effects of evolution

Evolution is likely to mediate the effects of climate change on species interactions and biodiversity (Hoffmann and Sgro, 2011; McEvoy *et al*., 2012; Norberg *et al*., 2012; Szűcs *et al*., 2012; Northfield and Ives, 2013). Directional selection from rising temperatures could benefit species with wide tolerances, allowing them to expand their ranges and dominance during climate change (Hoffmann and Sgro, 2011).

Evolution and co-evolution in predator–prey systems may non-intuitively alter predator–prey equilibria, with implications for biological control (Northfield and Ives, 2013). Some approaches to examining evolutionary effects include:

- Conduct longitudinal studies on populations surviving in different environments (Hoffmann and Sgro, 2011). This can include comparisons of thermal tolerance or behaviour of predator and prey along existing thermal or climatic continua for evidence of climate-driven selection on these traits (e.g. Harmon *et al*., 2009; Barton, 2011).

7.5.5 Allocation of limited resources: setting priorities

Because of the complexity and difficulty of the research required, efforts must necessarily focus on the most economically important and potentially climatically vulnerable or sensitive systems. Vulnerability or sensitivity may be greatest near the boundaries of the ranges of pests and natural enemies, which could shift with climate change, or where climatic constraints on the stability of biological control are already taking place. In addition to the vulnerability likely near the edge of climatic ranges, imperfectly aligned phenologies of trophically linked species can arise from various other ecological and evolutionary factors (Singer and Parmesan, 2010), and systems where alignments are already marginal may be more vulnerable to climate perturbations. Identifying these vulnerable systems will require identifying archived or newly acquired data. This remains a significant challenge.

7.5.6 Conclusion

Although we have focused as much as possible on North American agricultural systems in this review, we have occasionally drawn on examples from elsewhere or from forest systems, because data are sparse. None the less, the principles and needs discussed here pertain globally. It is our hope that this overview is helpful for addressing the implications of climate change for biological control in North America and elsewhere.

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8

Climate Change Effects on Agricultural Insect Pests in Europe

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Abstract

In this chapter, we will discuss observations of climate change effects on agricultural pests in Europe, the possible mechanisms behind these observed effects and finally delve into more detail through some relatively well-studied model species (the Colorado potato beetle and the rape beetle). Direct effects of climate change on agricultural pests in Europe are difficult to dissect from all the human-induced changes that have taken place in parallel with an increased mean annual temperature. During the past decade, agriculture has become more professionalized in terms of land use, crop cultivation techniques and pest management strategies. We review the effect of climate change on agricultural pests by comparing the speed of range expansion of pest species to non-pest species. It seems that the poleward range shift has been faster for pest than non-pest species. We attribute this partly to the globalization of agriculture as human-assisted movement has broken many natural dispersal barriers. Since the biology of many pest species is relatively poorly studied, direct conclusions on how climate change has affected the biological processes of pests are challenging to make.

8.1 Introduction

While climate change scenarios for European agriculture suggest both positive and negative effects, the net effects are calculated to be negative (Hyvönen, 2011; Hoye *et al*., 2013; Challinor *et al*., 2014). The effects depend on location, and future scenarios vary greatly for different parts of Europe. In northern Europe, mean temperatures are increasing (especially during winter and spring), and thus the immediate effects of climate change could be positive due to a prolonged growth season length (Myeni *et al*., 1997). Similarly, the predicted increase in air CO_2 and temperature can boost plant growth if the necessary water, nutrients and pest control are available (Wand *et al*., 1999). Indeed, in many countries, such as Finland, increasingly shorter development times of various crops have been documented during the past 50 years (Peltonen-Sainio and Hakala, 2014). In southern Europe, in turn, temperatures have been suggested to increase even more than the estimated average mean global temperature increase (Carraro and Sgobbi, 2008; IPCC, 2013). When this is accompanied by an increased frequency and severity of heatwaves and decrease in precipitation,

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the end result may be an increase of desertification rather than an increase of agricultural productivity.

Similarly as for plants, growth season length and thermal stress are among the most important factors also limiting ranges in many arthropods (Addo-Bediako *et al.*, 2002). Therefore, we can ask: what are the major predictions of the climate change responses of European pests? A longer, warmer growth season is expected to affect pests through increasing the time available for development and growth, provided that hosts or prey are also available or, put another way, provided that the pests have previously been temporally restricted (Bale *et al.*, 2002). Depending on the life history strategies of the pest, signs of climate change effects could be variable (see, for example, Musolin, 2007; Kingsolver *et al.*, 2011) and expected; for instance, in development time (Boman *et al.*, 2008), voltinism (the number of annual generations) (Altermatt, 2010) and the duration of the reproductive period (van Asch *et al.*, 2013). These changes in life history traits can have population consequences and lead to increased population sizes or enlarging or, alternatively, shifting ranges (Gaston, 2003; Bebber *et al.*, 2013; Bacon *et al.*, 2014). On the other hand, increased temperatures may also allow host plants to be able to protect themselves better against herbivory (DeLucia *et al.*, 2012), which again can reduce pest population sizes. Additionally, most major agricultural pest species are under continuous surveillance and actively controlled by humans when needed, and therefore might not be able to utilize fully the benefits of temperature increase and climate change.

In the present chapter, we summarize the observed effects of climate change on important agricultural insect pests in Europe. Many pests exist in complex, often non-natural conditions in agricultural systems. Climate change is expected to influence both the agricultural systems as well as the pests in both indirect and direct ways. Therefore, it can be challenging to show a causal connection between climate change and pest species biology. For the purposes of simplicity, we will divide climate change into both climatic effects (e.g. temperature, humidity), and anthropogenic effects, which mainly are responses to climate change (changes in agricultural practices, land use, human population sizes, transport pressure). Of these, direct climatic effects are more studied. In this chapter, we will discuss: the basis of the observation of climate effect; the possible mechanisms behind these observed changes; and, finally, delve into more detail through some relatively well-studied model species.

8.2 Observed Increase in Pest Introductions and Range Shifts Towards the Poles

Due to the negative impact pest species generally have on agriculture, there is an acute interest in monitoring and restricting the spread of pest species, as well as influencing their population dynamics. However, although many governmental and agricultural officials keep records (e.g. Genovesi and Scalera, 2011; Hyvönen, 2011; Vänninen *et al.*, 2011) of pest species in a given country and EPPO (The European and Mediterranean Plant Protection Organization) keeps a record of new introductions of many pests to Europe, systematic record keeping is fairly recent. This makes it hard to estimate the effect of climate change on European pests over long periods. Furthermore, the majority of the existing literature on climate change effects actually consists of predictions rather than observations (Cannon, 1998; Dupin *et al.*, 2011; Aragón and Lobo, 2012; Maiorano *et al.*, 2012; Stöckli *et al.*, 2012; Kroschel *et al.*, 2013; Jönsson *et al.*, 2013; Bacon *et al.*, 2014).

At the same time that changes in climate have taken place during the past 100 years (IPCC, 2013), agricultural practices have changed and become more professionalized. The productivity of agriculture has increased due to the increase in plant breeding programmes, fertilizer use and organized pest management monitoring and control. In Europe, there has been an organized plant protection practice since the establishment of EPPO in 1951. This means that there has been an early alert system, as well as organized quarantine practices for many pest species. This might have hindered pest species to respond to changes in climate and invade new areas unnoticed. However, within the past 30 years, in parallel with temperature increase, globalization and the associated large upscaling in trade has broken the natural dispersal barriers of many species (see, for example, Lebarbenchon *et al*., 2008). All these changes have happened at the same time, and disentangling the effects due to changes in climate from other changes is extremely difficult.

According to the latest assessment by the IPCC, mean annual temperatures have increased by approximately 0.85°C during the past 100 years, and will continue to increase under all envisioned climate change scenarios (IPCC, 2013). The observed increase in temperature has resulted in range enlargements or shifting of the entire range towards higher latitudes or altitudes in many non-pest species (Parmesan *et al*., 1999; Walther *et al*., 2002; Chen *et al*., 2011). The speed of climate change-dependent range shifts varies depending on the species group as well as the time investigated (see Table 8.1; Hickling *et al*., 2006; Bebber *et al*., 2013). The first estimates of range shifts of several non-pest species suggest that the speed has been on average 6.1 km/decade (Parmesan and Yoche, 2003), whereas recent estimates, at least for butterflies, suggest a speed ten times faster (e.g. Pöyry *et al*., 2009). For non-pest butterfly species in northern Europe, dispersal ability together with habitat availability has been suggested to play major roles in the range expansions observed (Pöyry *et al*., 2009). This and other studies highlight that species' life history traits are imperative to consider when assessing their capacity to respond to climate change (Saikkonen *et al*., 2012; Breed *et al*., 2014; Mair *et al*., 2014). While most studies on responses to climate change have focused on non-pest species, these results may also be used as tools to estimate the effects for numerous pest species (Bebber *et al*., 2013).

The range shifts of pest species has recently been estimated from 612 species, including fungi, bacteria and viruses, in addition to arthropods, by Bebber *et al*. (2013). This study shows a poleward shift of pests that is 27 km/decade since the 1960s, and therefore it seems that range shifting has been significantly faster in pest species than for non-pest natural arthropods (Table 8.1). So, can agricultural pests respond to climate change faster than non-pest species? To dissect the effect of climate change on the range expansion of many pest species from other anthropogenic effects, such as land use (Kalnay and Cai, 2003) or human-assisted movement (Smith *et al*., 2007), is, as stated, challenging. During the past 100 years, massive changes in agricultural policies and other anthropogenic factors have taken place. These include pesticide use, together with quarantine regulations (see Bacon *et al*., 2014), which should both hinder pest range shifts due to constant control of pest population size. On the other hand, the transport of goods has, in turn, increased the interconnectivity of the globe, which should increase the rate of range expansion of many pathogens and pests (Lebarbenchon *et al*., 2008) due to enhanced propagule pressure (Mack *et al*., 2000; Tatem and Hay, 2007). Indeed, it has been shown that the ornamental plant trade is one major contributor to the introduction of new plant pests to European countries (Smith *et al*., 2007). This is probably because an increase in trade elevates propagule pressure and makes introductions more frequent. In the UK, it is estimated that 70% of the pest species established since 1970 have been assisted by humans, while only 30% have managed to establish on their own (Smith *et al*., 2007). Similarly, EPPO records show that there is actually an increase of new pest records in Europe (Fig. 8.1), although it is unknown whether this is related to the changes in climate or changes in human transport (EPPO, 2013a).

An additional problem is that the same pest species is imported from several places at the same time. This can be illustrated with an example of a quarantine pest, the silverleaf whitefly, *Bemisia tabaci*. In 2013 alone, a significant number of *B. tabaci* individuals were detected in shipments of imported

Table 8.1. Average range shifts of both pest and non-pest insect species collected from various meta-analyses published during the last decade. The observation time (as recorded in the given literature) and the rate of range shifts (kilometres/year, ±standard error of mean) within the observed period. The number of species is given in brackets.

	Pest species		Non-pest species			
Observation time	*c.*1920–2010	1960–2010	*c.*1965–1990	1992–2000	*c.*1920–2000	Variable
	Rate[a] km/year±SE (sp)	Rate[a] km/year±SE (sp)	Rate[b] km/year±SE (sp)	Rate[c] km/year±SE (sp)	Rate[d] km/year±SE (sp)	Rate[e] km/year±SE (sp)
Coleoptera	7.61±1.87 (70)	12.21±4.33 (70)	2.48±0.43 (86)			
Diptera	3.11±2.48 (24)	3.95±6.08 (24)				
Hemiptera	6.13±3.25 (47)	13.71±5.32 (47)				
Hymenoptera	4.60±9.48 (6)	8.11±11.64 (6)				
Isoptera	19.62±10.83 (1)	–7.51±13.89 (1)				
Lepidoptera	8.00±2.71 (36)	17.78±8.58 (36)	1.76±0.46 (29)	7.49±1.75 (48)		
Neuroptera			1.76±1.16 (6)			
Odonata			4.16±0.68 (20)			
Orthoptera			1.36±0.32 (22)			
Thysanoptera	7.68±4.36 (3)	1.06±9.31 (3)				
Overall		2.7±0.8 (600)	1.74±0.82 (329)		0.61± 0.24 (99)	1.76±0.29 (764)

Notes: [a]Bebber *et al*. (2013) estimates based on CABI records. [b]Hickling *et al*. (2006) estimated from different UK species, times vary; [c]Pöyry *et al*. (2009) estimated from Finnish butterflies; [d]Parmesan and Yoche (2003) includes also birds, herbs and butterflies; [e]Chen *et al*. (2011) based on several published meta-analyses.

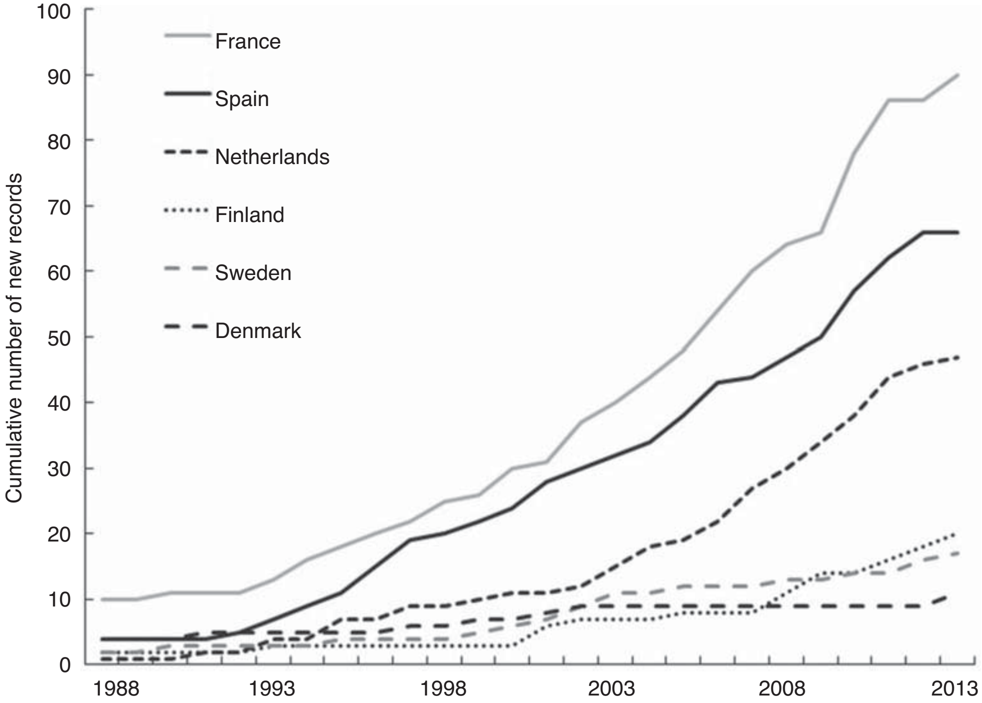

Fig. 8.1. Cumulative number of new records of pests in six Western European countries. (From EPPO, 2013b.)

vegetables and ornamentals in the UK. These individuals were brought to the UK from 14 countries on four continents (EPPO, 2013a; Fig. 8.2), which could result in the introduction site harbouring higher genetic variability than any of the original or native sites (Kolbe *et al*., 2004). This is part of the reason why, for instance, tree nurseries in Europe can act as gateways for many plant pathogens in Europe (Santini *et al*., 2013). Seedlings are brought to nurseries from various parts of the globe, together with their plant pathogens. Therefore, it is possible that in the nurseries, different disease strains meet and hybridize, resulting in high genetic variability of the plant pathogens. When these seedlings are then sold to various parts of Europe, the pathogens are exported to large areas. Although we will observe a shift in ranges of these pathogens or pests, this is not necessarily due to climate change but rather due to human activities in the 21st century. As an aside, forest pathologists have formulated 'the Montesclaros Declaration', which states that: 'We thus propose a phasing out of all trade in plants and plant products determined to be of high risk to forested ecosystems but low overall economic benefit' (see Santini *et al*., 2013).

8.3 Can Changes in Winter Biology Explain Changes in Pest Biology?

Winter temperatures are predicted to be influenced more strongly by future climate change than summer temperatures (IPCC, 2013). Since winter abiotic and biotic conditions are major factors governing arthropod biology in Europe, less severe and shorter winters in the future could have a major impact on pest species population and range dynamics (Bale and Hayward, 2010). In a recent study, the range shifts in non-pest butterflies in Finland were found to relate to the stage in which the species overwintered (Pöyry *et al*., 2009). Species that

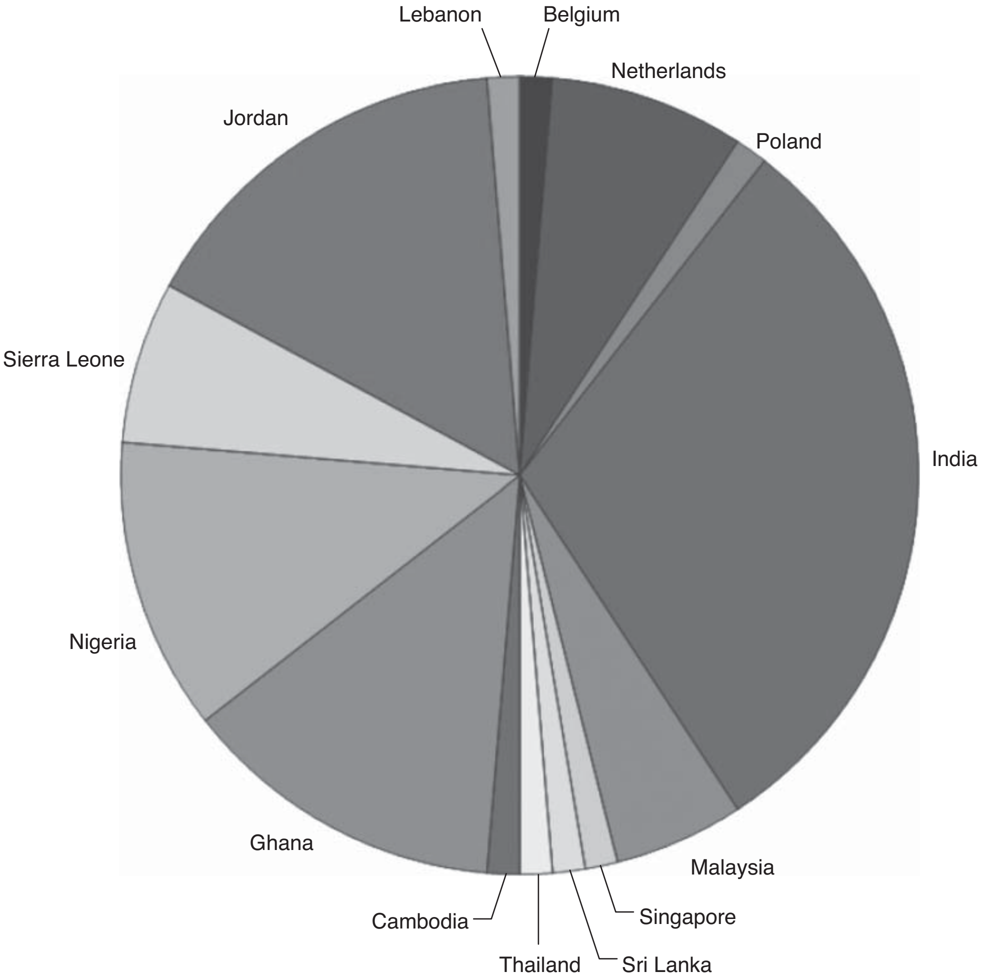

Fig. 8.2. Proportion of *Bemisia tabaci* individuals found on ornamentals and vegetables from the UK divided according to country of origin. (From EPPO, 2013a; *N*=76.)

overwintered as adults were found to have expanded their ranges at a higher rate than those that overwintered in other stages. This could be related to the fact that adults can prepare for winter more easily, for instance through microhabitat selection, or it is easier for adults to adapt to changes in the photoperiod (Lehmann *et al*., 2012; Saikkonen *et al*., 2012).

Although seasonal temperature averages and fluctuations are predicted to change in the future, photoperiodic cycles will remain the same. As Europe is located in the temperate seasonal zone, any species invading Europe, or which can expand its range in Europe, should also be able to adapt to the changing relationship between photoperiod and season. In temperate zones, the life cycles of arthropods as well as their hosts are generally governed by large seasonal fluctuations (Tauber *et al*., 1986). The season can be characterized by a division into two phases, where summers constitute the active and winter the non-active phase. This means that the species which respond to changes in temperature by invading northwards have to be able to synchronize their life cycle with the new local seasonal cycle (Bradshaw and Holzapfel, 2001; Bradshaw *et al*., 2004). For arthropods, the observed range shifts have been attributed to a release of thermal stress (Ammunét *et al*., 2012), as well as seasonal resynchronization of life history (Gaston, 2003; Bean *et al*., 2012; Saikkonen *et al*., 2012). This may require adaptive changes, and ultimately the range shifts are then dependent on the genetic variability within the species (e.g. Piiroinen *et al*., 2011).

To highlight some recent research and observations on insect pest species in Europe, we chose to investigate beetles (Coleoptera) in more detail. Beetles are among the most diverse insect taxa, and several important pests are beetles, most notably in forestry, but also in agriculture and horticulture (Bebber *et al*., 2013). These include, for instance, the Colorado potato beetle, *Leptinotarsa decemlineata* (Alyokhin, 2009), and the Western corn rootworm, *Diabrotica virgifera* (Dupin *et al*., 2011). Table 8.2 lists some of the most important beetle pests found in agricultural and horticultural systems in Europe (Bebber *et al*., 2013). As can be seen, the best-represented families are Curculionidae (true weevils or snout beetles), Cerambycidae (longhorn beetles) and Chrysomelidae (leaf beetles). Of these insects, 26 feed primarily on wood, 11 on soft plant tissue (including leaves, fruits, flowers, tubers) and 1 is carnivorous. The majority (78%) of these beetles have a dedicated overwintering stage, which in 72% is the adult stage. Interestingly, comparing ranges of beetle pests found in Europe with beetle pests whose ranges do not include Europe (listed in Bebber *et al*., 2013) reveals that pests whose range includes Europe are found over a larger latitudinal range (mean = 77.6°, SEM = 6.2) than those whose range excludes (mean = 55.0°, SEM = 4.5) Europe (two-tailed t-test: $t_{66.2} = 2.43$, $P = 0.018$). This could indicate a sampling bias, since European (together with North American) countries generally use more resources to track and report pest movements (e.g. EPPO, NAPPO, etc.), but the involvement of some biological mechanisms cannot be ruled out.

While some species clearly have enlarged their ranges during the past 100 years, there are several examples of beetle species that seemingly have not responded through range shifts or changes in population dynamics (voltinism, population size). In fact, of the 37 beetle species occurring in Europe that were studied by Bebber *et al*. (2013), only two showed a significant range expansion or shift since 1960, while the absolute majority showed no significant shift (Table 8.2). Since temperatures have increased, growth seasons become longer and the winter shorter, the majority of species have likely not been restricted by temperature previously, but more likely by other factors that are temperature independent, such as pesticide use, for instance. Therefore, it is important to consider the difference between climatic unsuitability and invasion dynamics when trying to estimate whether species occur where they do due to climate change. For example, as stated by Dupin *et al*. in their study (2011): ‘Only presence data (ed. of *Diabrotica virgifera*) were considered in Europe as the range of the pest is still expanding and hence absences from this region may not be an indication that the climate is unsuitable.’

Although the poleward range shift for Coleoptera was estimated to be 12.2 km/year in the data collected by Bebber *et al*. (2013), only two species showed significant, climate change-driven enlargements of their range. These were the Emerald ash borer, *Agrilus planipennis*, and the Red palm weevil, *Rhynchophorus ferrugineus*, both serious wood-feeding forest pests (Bebber *et al*., 2013). *A. planipennis* feeds on various *Fraxinus* species and has a distribution covering most of northern Asia, including European Russia (Baranchikov *et al*., 2008) and North America, where it was introduced in the beginning of the 21st century (EPPO, 2005). Larvae feed in the cambium of trees or in the stems of smaller woody plants and will ultimately kill attacked trees. While still absent from the EU, despite several interceptions, the likelihood that the species could establish itself is considered very high (EPPO, 2005; Baranchikov *et al*., 2008). While *A. planipennis* is native to Far East Russia and thus adapted to seasonal environments, *R. ferrugineus* is native to the tropics and has expanded its range into seasonal

Table 8.2. Major coleopteran pests found in Europe with some of their important biological traits. Data were gathered from EPPO and CABI. A generalist species is defined as a beetle with over five host plant species. Latitudinal range was estimated based on Bebber *et al*. (2013). Some species are less well studied, and a question mark denotes that uncertainty exists regarding that particular trait or that references are contradictory. Two species (*Agrilus planipennis* and *Rhynchophorus ferrugineus*) have significantly enlarged ranges due to climate change, according to Bebber *et al*. (2013). All species occur in outdoor fields except for *Scyphophorus acupunctatus*, which is limited to greenhouses, and some species that occur both in outdoor fields and greenhouses (marked with * after the species name).

Species	Family	Origin	Horticultural (H) or agricultural (A)	Feeds on wood	Generalist (G) or specialist (S)	Overwinters in diapause	Over-wintering stage	Latitudinal range (°)[a]	Number of references in WoS[b]
*Acanthoscelides obtectus**	Chrysomelidae	Neotropical	A	N	G	Y?	Adult?	7.1	356
Agrilus planipennis	Buprestidae	Eastern Asia	H	Y	S	Y	Prepupa	127.8	236
Anthonomus bisignifer	Curculionidae	Japan	H	N	S	Y	Adult	28.4	0
A. pomorum	Curculionidae	Palearctic	H	N	S	Y	Adult	35.5	35
Callidiellum rufipenne	Cerambycidae	Eastern Asia	H	Y	G	Y	Pupa	120.7	13
Cylas formicarius	Brentidae		A	N	S	N[c]	Adult	85.2	197
Diabrotica virgifera	Chrysomelidae	North America	A	N	S	Y	Egg	30	700
Diocalandra frumenti	Curculionidae	Australia	H	Y	S	N		78.1	1
Gonipterus scutellatus	Curculionidae	Australia	H	Y	S	Y	Adult	113.6	39
Harmonia axyridis	Coccinellidae	Central and Eastern Asia	A	N	G	Y	Adult	120.7	850
Hylobius abietis	Curculionidae		H	Y	G	Y	Larva	127.8	310
Hylotrupes bajulus	Cerambycidae	Europe	H	Y	S	N[c]	Larva	127.8	90
Hylurgus ligniperda	Curculionidae	Europe	H	Y	S	Y	Adult	131.35	29
Hypothenemus hampei	Curculionidae	Central Africa	H	N	S	N		78.1	293
Ips cembrae	Curculionidae	Europe	H	Y	S	Y	Adult	134.9	24
I. sexdentatus	Curculionidae		H	Y	S	Y	Adult	63.9	95
I. subelongatus	Curculionidae		H	Y	S	Y	Adult	39.05	14
I. typographus	Curculionidae	Europe	H	Y	S	Y	Adult	35	787
Leptinotarsa decemlineata	Chrysomelidae	Mexico	A	N	S	Y	Adult	71	1592

continued

Table 8.2. *continued.*

Species	Family	Origin	Horticultural (H) or agricultural (A)	Feeds on wood	Generalist (G) or specialist (S)	Overwinters in diapause	Over-wintering stage	Latitudinal range (°)[a]	Number of references in WoS[b]
Lilioceris lilii	Chrysomelidae		H	Y	S	Y	Adult	49.7	17
Listroderes costirostris	Curculionidae	South America	A	N	G	N[c]	Prepupa	110.05	6
Megaplatypus mutatus	Curculionidae	Neotropical	H	Y	G	Y?	Larva	99.4	12
Meligethes aeneus	Nitidulidae	Holarctic region	A	N	G	Y	Adult	49.7	175
Monochamus galloprovincialis	Cerambycidae	Eurasia	H	Y	S	Y?	Larva	49.7	54
M. sutor	Cerambycidae	Eurasia	H	Y	G	Y	Larva and pupa	49.7	11
*Phaedon brassicae**	Chrysomelidae	East and South Asia	A	N	G	Y	Adult and larva?	35.5	12
Phoracantha recurva	Cerambycidae	South-east Asia	H	Y	S	N?		106.5	20
P. semipunctata	Cerambycidae	Australia	H	Y	S	N?		127.8	88
Pissodes castaneus	Curculionidae	Europe	H	Y	G	Y	Larva, adult	49.7	22
Rhynchophorus ferrugineus	Curculionidae	South-east Asia	H	Y	G	N?	Adult	78.1	131
Saperda candida	Cerambycidae	Costa Rica	H	Y	G	Y?	Larva	35.5	0
Scolytus morawitzi	Curculionidae	Asia	H	Y	S	Y	Larva	28.4	0
S. schevyrewi	Curculionidae	Eastern Asia	H	Y	G	Y?	Larva, adult	35.5	13
Scyphophorus acupunctatus	Dryophthoridae	New World	H	N	S	N?		63.9	22
Sinoxylon conigerum	Bostrichidae		H	Y	G	Y	Adult	85.2	1
Xylosandrus crassiusculus	Curculionidae	South-east Asia	H	Y	G	N?		78.1	26
X. germanus	Curculionidae	East Asia	H	Y	G	Y	Adult	85.2	37
Xylotrechus altaicus	Curculionidae	Asia	H	Y	S	Y	Larva	21.3	0

Notes: [a]Resolution was 7.1°; [b]Web of Science (WoS) Available at: http://apps.webofknowledge.com/ (accessed 24 April 2014); [c]non-diapause dormancy.

environments only relatively recently (EPPO, 2008). As can be deduced from its common name, *R. ferrugineus* feeds on various palm trees. Currently, it is found in most of southern Europe, where palm trees are cultivated both commercially and for ornamental purposes. While a serious pest in the tropics, it is less of a problem in Europe, due primarily to the relatively small scale of palm cultivation.

8.4 Model Systems in More Detail

8.4.1 The Colorado potato beetle and the rape beetle

What is evident from the literature search on the pest species we list in Table 8.2 is that we know very little of the basic biology of many of them. Therefore, it is difficult to actually document changes that might have taken place due to climate change. We have therefore chosen two pest species that are relatively well studied and ask how climate change has affected their range expansion dynamics or general biology within ranges. The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), was chosen as its range expansion has been well documented in the past; it originates from low latitudes in North America and thus its high-latitude range expansion has potentially been restricted by temperature. The rape or pollen beetle, *Meligethes aeneus* (Fabricius) (Coleoptera: Nitidulidae), is, in turn, native to Europe and its expansion potential might be related to the indirect effects of climate change.

8.4.2 The range expansion of the Colorado potato beetle across the northern hemisphere

The rapid range expansion of *L. decemlineata* across most of the northern hemisphere has been very well documented (Johnson, 1967; EPPO, 2014). *L. decemlineata* originally stems from northern Mexico and has, in around 200 years, transformed from a low-density, low-latitude, non-pest species to a high-density, high-latitude, commercially significant pest species (Alyokhin, 2009). In this section, we will outline briefly the life and expansion history of *L. decemlineata* and attempt to answer whether its range expansion has been driven or influenced by ongoing climate change and how climate change is expected to affect established populations at different latitudes.

L. decemlineata was discovered and named by Thomas Say in the early 19th century (Say, 1824). The then described leaf beetle was just one of a group of 30-odd closely related chrysomelids living in rather low-density populations in central America and the south-western part of the USA. This changed dramatically when potato, *Solanum tuberosum*, was introduced into the southern states of the USA as a crop between 1840 and 1850. Soon afterwards, some of the native *L. decemlineata* shifted host plants from the local potato relative Buffalo bur, *Solanum rostratum*, to potato and became invasive. The first American state where a major outbreak occurred was Colorado, which is the origin of the beetle's common name (Casagrande, 1987). Today, *L. decemlineata* is the most important insect pest of potato found in an area covering 16 million km^2 from Mexico, through North America, to most of Europe and deep into Asia (Johnson, 1967; Alyokhin, 2009; EPPO, 2014).

The capacity of *L. decemlineata* adults to burrow into the soil for overwintering in diapause (e.g. Hsiao, 1985) is probably among the most important features that have assisted its range expansion into high-latitude habitats (EPPO, 2014). Diapause is a deep resting stage that normally lasts one winter season, but can also be prolonged and can last up to 9 years (Tauber and Tauber, 2002). Another interesting characteristic is that around 20% of all newly eclosed adults in every thus far studied population enter diapause regardless of environmental conditions (Danilevskij, 1965; Hsiao, 1985; Tauber *et al.*, 1986; de Kort, 1990). As *L. decemlineata* is a major pest of potato, quarantine inspections and regulations have hindered its spread (first notification in Europe, 1875, permanent populations, 1922). It was likely that deregulation of concerted pest management during the First World War was pivotal in allowing the beetle to establish in France. The beetle has further been heavily selected by pesticides, as chemical control of population densities has been employed forcefully throughout its range. The species is very capable of resisting pesticides, which probably is due partly to the natural toxicity of the alkaloids of the host plant, potato (see discussion in Piiroinen *et al*., 2013), and also to the rapid evolution of resistance against new pesticides (Alyokhin, 2009). Indeed, *L. decemlineata* is justifiably called a super-pest due to the many features (fecundity, dispersal, overwintering and pesticide resistance) that have made containment and management very challenging (Hsiao, 1985; Alyokhin, 2009).

The annual expansion distance of *L. decemlineata* has been estimated to be between 80 and 130 km in North America and Europe (Walsh, 1865; Tower, 1906; Johnson, 1967; EPPO, 2014). The original historic spread of *L. decemlineata* across North America from relatively low latitudes in Nebraska (41°N), where the first major outbreak took place in 1859 (Tower, 1906), to 50°N in Canada, 1901–1911, took place during a time when little change in ambient temperature occurred (IPCC, 2013). Consequently, it was likely that this spread was facilitated by habitat availability, dispersal ability, plastic life history strategies and local adaptation to pronounced seasonality at higher latitudes (Hsiao, 1985) rather than changes in climate. In Europe, in turn, the beetle has invaded northwards at a rate of approximately 28.6 km/year since the 1920s, when the population was considered established in Europe in France (44°N), to its current northernmost latitude of around 61°N in 1970. Thus, it has expanded its range at a much faster rate than non-pest species responding to climate change (Table 8.1), which suggests that human involvement has been important.

Several studies on European and North American *L. decemlineata* populations suggest rapid divergence of adaptive variation in life history and physiological traits (e.g. Danilevskij, 1965; Hsiao, 1985; Boman *et al*., 2008; Lehmann *et al*., 2012; 2014a; Lyytinen *et al*., 2012; Izzo *et al*., 2014). The question is whether these changes are driving range expansion or whether local adaptations arise secondarily after successful establishment (see Urbanski *et al*., 2012), which occurs primarily without adaptation, through, for instance, plasticity or broad general stress tolerance (Lehmann *et al*., 2014b). The range expansion of *L. decemlineata* in northern Europe has slowed down during the past 30 years (EPPO, 2014). This could be due to many factors, including a shorter growth season and a longer and harsher winter, or due to a low genetic variability (Grapputo *et al*., 2005). It is unlikely that a short and cold growth season is strongly limiting expansion, since genetic variability still exists in growth-related traits (Boman *et al*., 2008; Lyytinen *et al*., 2008). At northern latitudes, the progressively harsher winter is a likely expansion barrier (Valosaari *et al*., 2008; Piiroinen *et al*., 2011). It is possible that plasticity in avoidance behaviour, which might have assisted in expansion in more benign environments, fails to provide enough thermal buffering at high latitudes, thus requiring local adaptation (Lehmann *et al*., 2014b). The retardation of expansion is therefore probably due to an inability to respond to selection, as high-latitude populations show a low amount of heritable variation in physiological traits important for winter survival (Piiroinen *et al*., 2011).

During the past 100 years, in parallel with the range expansion of *L. decemlineata*, climate has warmed by approximately 0.85°C (IPCC, 2013). Has this increase in temperature had a meaningful impact on the range expansion propensity of the beetle? Many life history traits in *L. decemlineata* have been shown to depend on temperature, such as development time (Boman *et al*., 2008), dispersal capacity (Caprio and Grafius, 1990) and the decision to enter diapause (Danilevskij, 1965). While most of these traits are affected positively by increased temperature, the decision to enter diapause is more complex, since increased temperature decreases diapause propensity

(Danilevskij, 1965), thus potentially increasing the ovipositing period of beetles. Since late summers are associated with higher climatic variability, especially at high latitude, under current climate change scenarios the decision to prolong the reproductive period can have negative consequences for beetles. Furthermore, warmer winters mean less snow cover, which, combined with wetter conditions, means that low temperatures can penetrate deep into the soil more easily, potentially increasing overwintering mortality of diapausing beetles (Boiteau and Coleman, 1996; Costanzo *et al*., 1997, 1998; Groffman *et al*., 2001).

Taken together, we think it is unlikely that *L. decemlineata* has been affected significantly by climate change-related ambient temperature increase in its expansion thus far (see supplement in Bebber *et al*., 2013). Future expansion and population dynamics in established populations might show both positive and negative associations with increased temperature (see, for example, Milner *et al*., 1992). In case winters become more benign (shorter, warmer), a major potential obstacle for spread to higher latitudes in Europe may disappear (Jönsson *et al*., 2013). Furthermore, many models predict fairly rapid responses in increased voltinism in European *L. decemlineata* populations, in case growth season and, importantly, potato growing season increases in length significantly (Valosaari *et al*., 2008; Jönsson *et al*., 2013). Therefore, we stress that care must be taken when partitioning out the effect of climate change in driving historical, current or future range expansion in pest species.

8.4.3 Population dynamics of the rape beetle, *Meligethes aeneus*, at high latitudes in Europe

The rape beetle, *Meligethes aeneus*, is a common beetle occurring in most of the holarctic region (Alford, 2003). It feeds on a range of naturally occurring plants, especially Brassica and Sinapis species, and is not considered particularly harmful when on natural plants. However, since it also uses commercially grown rape crops as hosts, it has the potential to become a serious pest with a large economic impact. Populations of *M. aeneus* are generally univoltine, and adults overwinter as adults in woodlands. Due to their high protein content, rape crops (*Brassica napus*, *Brassica rapa*) increasingly have been appreciated as animal feed, and an increasing interest in biofuel applications (Tiilikainen and Hokkanen, 2008) have further increased the attractiveness of growing rape. Indeed, rape is one of the most important crop plants in Europe, with a total production volume of 19×10^{6} t grown during 2010–2011 in the EU (Eurostat Pocketbooks, 2012). At high latitude in Europe, such as Finland, *B. rapa* has traditionally been favoured over *B. napus*, due to shorter growth season requirements (Peltonen-Sainio *et al*., 2009). The increasing utilization potential of rape has led to the development of more cold-tolerant and hardy high-latitude variants that can be found in northern Europe (Mäkelä *et al*., 2011). This has led to shifts in the prevalent or preferred variant of rape in northern growing regions (*B. rapa* spp. *oleifera* becoming more common, while the more traditional *B. napus* spp. *oleifera* has become less common). Shifting to a hardier variant has allowed rape crop rearing at higher latitude and at higher areals (Peltonen-Sainio *et al*., 2009). Indeed, the total cultivated area of different rape species has increased by several orders of magnitude in Finland during the past 50 years (Fig. 8.3). The increased growing areals of rape crops has had positive effects on *M. aeneus*, which also has increased in abundance in concert with its host plant (Tiilikainen and Hokkanen, 2008) (Fig. 8.3).

Both adult and larval *M. aeneus* can damage rape crops. The adults can eat the flowers and supporting structures, while larvae eat pollen within buds and flowers. In cases where populations are not controlled, yield losses in commercial rape crops can be up to 70% (Nilsson, 1987). *M. aeneus* is widely controlled both through biological (Veromann *et al*., 2006) and, more commonly, chemical means (Smatas *et al*., 2012).

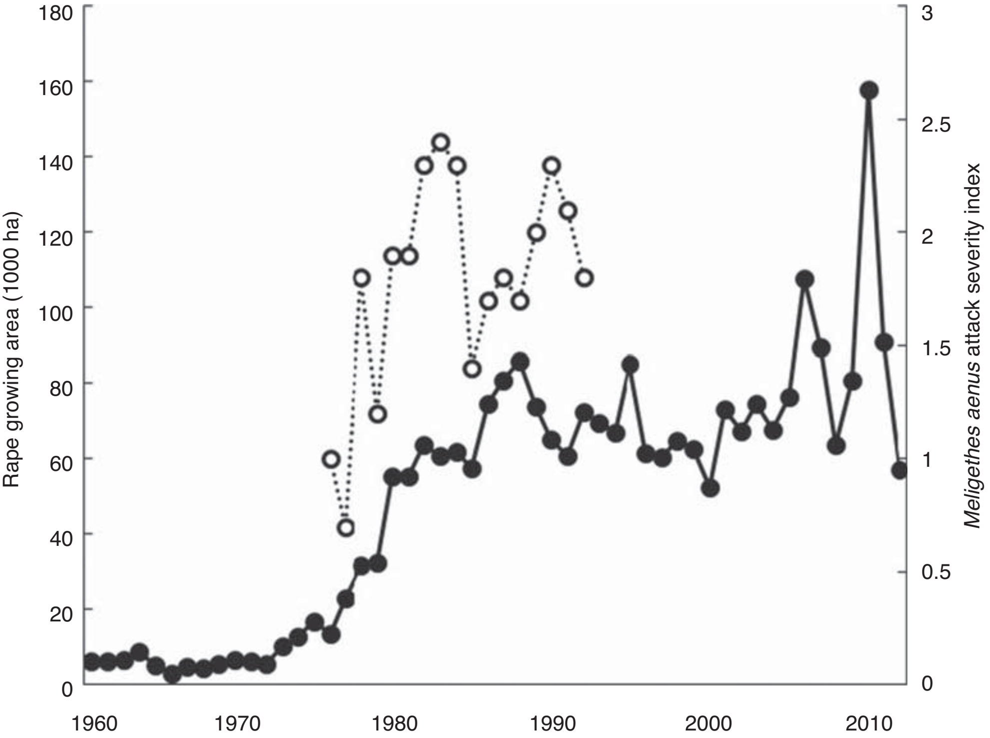

Fig. 8.3. The solid line shows areas of rape grown in Finland, 1950–2010. During 1950–1970, the predominant rape variant was winter turnip rape (*Brassica napus* spp. *oleifera*), while the increase after 1970 to the present day constitutes primarily spring turnip rape (*Brassica rapa* spp. *oleifera*) substituting winter turnip rape. The dashed line shows the severity index of *Meligethes aeneus* attacks estimated in southwestern Finland between 1977 and 1992. (From Mäkelä *et al*., 2011, and Hokkanen, 2000.)

Chemical management is complicated by high levels of pesticide resistance (Tiilikainen and Hokkainen, 2008; Smatas *et al*., 2012), which is exacerbated by host shifts of *M. aeneus* individuals from commercially grown rape crops to wild relatives (Hokkanen, 2000). This shifting of host plants can increase spatial heterogeneity and contribute to the maintenance of large potential genetic variation in populations.

The effect of climate change is difficult to estimate in *M. aeneus* since this univoltine species already has a more northern distribution than its crop host plants. Therefore, climate change effects appear to be indirect as warming affects the range of its host plant range, rape being cultured at higher latitudes and in larger areas. According to Bebber *et al*. (2013), *M. aeneus* has not shifted or enlarged its range during the past 60 years; however, its severity has increased, primarily through an enlargement in host plant planting areas and increasing pesticide resistance (Tiilikainen and Hokkainen, 2008; Smatas *et al*., 2012). According to Hakala *et al*. (2011), climate change might make the cultivation of different rape variants possible as far north as Lapland by 2085. If this is the case, *M. aeneus* most likely will transition along with its host, and increase in severity as a pest.

8.5 Conclusions

The fifth IPCC report (IPCC, 2013) presents, clearer than at any time before, evidence supporting the dynamics of ongoing climate change. Therefore, the general emphasis has already shifted from merely predicting climate change, into discussing means to mitigate damage due to already occurred or currently occurring climate change (see, for example, Carraro and Sgobbi, 2008). For agriculture, this means that across the globe, both governmental and non-governmental groups are calling for more information for more strongly integrated pest management and discussion of various adaptation strategies, since climate change already is apparent in many European agricultural systems (Genovesi and Scalera, 2011; Vänninen *et al*., 2011).

The observed climate change effects include both direct (loss of thermal constraints) and indirect (changes in habitat, species interactions, host plant ranges, etc.) effects, which are often hard to dissect from other anthropogenic effects (pesticide usage, assisted dispersal). There is also very little systematic information on the population sizes of a given pest over large areas for long periods, which makes it difficult to observe the changes in the first place. What is needed is a more systematic record keeping or a unifying Europe-wide database, similar to what is available already for non-pest species (see, for example, *Atlas of Finnish Macrolepidoptera*, Huldén *et al*., 2000). For instance, the citizen science application used to detect and monitor the invasion of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the UK (http://www.ladybird-survey.org/default.aspx) might be a possible application that could also be beneficial for agricultural professionals. Finally, effective utilization of the Internet with rigorous data selection criteria also allows us to utilize available databases (EPPO, NAPPO, CABI) more thoroughly, as recently seen in Bebber *et al*. (2013). Taken together, these various systematic approaches should provide the necessary tools to predict better the likely responses of pest species to climate change. The goal should be to develop means for horticultural and agricultural stakeholders to mitigate more effectively the negative impact that current and future climate change might have through changes in pest species biology.

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9

Abiotic Factors, Climatic Variability and Forest Insect Pests

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Abstract

Abiotic factors have both direct and indirect effects on insects. This chapter focuses on the direct effects of abiotic factors, especially temperature, on insects with different life histories. We draw examples from forest insect pests, mainly from temperate and boreal regions. We also illustrate and discuss several issues relevant for modelling the direct effects of climatic factors on forest insect pests. Abiotic factors can affect the mortality of forest pests in different life stages. Insects are generally well adapted to average conditions during different seasons, but extremes can cause problems. Examples are given from forest defoliators and aphids on conifers. Outbreak distribution and frequency in relation to climatic factors is discussed, with examples from both North America and Europe: the forest tent caterpillar, the spruce budworm and the European pine sawfly. The spatial and temporal resolution used when analysing forest insect outbreaks has often been at greatly larger scales than those at which the relevant ecological processes operate. Consequently, for further work, we stress the importance of considering spatial variation in temperatures when modelling the effects of changing climate on forest pests. Between-year variation in climate is often large in temperate and boreal areas. Examples of the relationships between abiotic factors and forest insects illustrate the multiple ways in which weather can modulate population dynamics. Finally, we discuss the possibilities for predicting the effects of changing abiotic factors on forest insect outbreaks. Multidisciplinary cooperation between researchers in different fields is urgently needed to bridge the gaps between the scales of insect pest dynamics, climate models and data. This is necessary to understand better the impacts of variable and changing climate on forest insect pests.

9.1 Introduction

Changing temperatures have been recognized as the dominant abiotic factor directly affecting herbivorous insects, while most other abiotic factors (e.g. CO_2, UVB, precipitation, wind) apparently do not have measurable direct effects, or they have been neglected in climate change research (Bale *et al*., 2002; Weed *et al*., 2013). The effects of changes in abiotic factors cannot be predicted solely by their direct effects on a species, but the indirect effects via trophic interactions should be considered as well (e.g. Lawton, 1994; Davis *et al*., 1998; Virtanen and Neuvonen, 1999a). The complex interactions between abiotic factors and the host plants and natural enemies (cf., for example, Stamp, 1993; Hance *et al*., 2007) are not reviewed here, but they are discussed

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in specific cases when appropriate, and more examples are described in other chapters of this volume (especially in Kalinkat and Rall, Chapter 5; Raffa *et al*., Chapter 10; Ammunét *et al*., Chapter 13, this volume).

Our chapter focuses on the direct effects of abiotic factors, especially temperature, on insects with different life histories. We draw examples from forest insect pests, mainly from temperate and boreal regions. We also illustrate and discuss several issues relevant to understanding and modelling the direct effects of climatic factors on forest insect pests. Understanding and predicting the effects of changing climatic factors on forest pest populations requires (based on/modified from: Kingsolver, 1989; Lawton, 1994; Logan *et al*., 2003):

1. Sufficient ecophysiological knowledge about the critical periods in the life cycle of the insect species and how abiotic variables affect insect performance (survival, development times, voltinism).
2. Estimating microclimates and insect body temperatures.
3. Considering other habitat attributes (forest composition and age structure, habitat fragmentation, etc.).
4. Understanding the density-dependent feedbacks (including trophic interactions) in the population dynamics of the target pest and how the effects of exogenous factors modulate them.
5. Information about past and current climate (different weather variables) with sufficient temporal and spatial resolution.

Considering the first ‘step’ (ecophysiological knowledge), many important forest pests have been well studied for decades, both in the laboratory and in the field, but in specific cases, significant new knowledge has been gained only quite recently (Tran *et al*., 2007; Régnière *et al*., 2012). In this chapter, we follow the above points loosely, starting with the effects of abiotic factors on forest insect pests and outbreak distribution. We also stress the importance of microclimates and spatial variation in temperatures (points 2 and 5 above) and give examples of the relationships between abiotic factors (weather) and forest insect population dynamics (point 4 above). Finally, we discuss the possibilities for predicting the effects of changing abiotic factors on forest insect outbreaks (points 4 and 5 above).

9.2 Abiotic Factors Affecting Forest Pests During Different Seasons

Abiotic factors can affect the mortality of forest pests in different life stages and in different ways. Insects are generally well adapted to average conditions during different seasons, but extremes can cause problems. However, insects have several adaptations to overcome the hazards during unfavourable seasons, which is generally winter in temperate and boreal regions. Adaptations for overwintering successfully are numerous and are reviewed, for example, by Leather *et al*. (1993) and Bale and Hayward (2010). In addition to causing direct mortality, extreme weather events (e.g. late frosts) may destroy host foliage and cause later mortality or poor performance due to lack of high-quality food.

Diapause enhances cold tolerance in most insects, and the diapausing stage is generally fixed and specific within a species (Bale and Hayward, 2010). However, there can be intraspecific geographical variation in the main overwintering stage. In hemimetabolous insects, eggs are generally more cold hardy than nymphs or adults, and in, for example, the green spruce aphid, *Elatobium abietinum* (Walker), holocyclic (overwintering as eggs) versus anholocyclic (overwintering as nymphs or adults) populations dominate in continental versus maritime areas.

The overwintering stage, associated with the microhabitat where it spends the winter, has prominent effect on the temperatures to which the insects are exposed during winter. Overwintering eggs in the canopy are exposed to ambient temperatures, while larvae or pupae in the litter are potentially covered by insulating snow, thus avoiding exposure to cold temperatures. There is also seasonal variation in egg cold-hardiness (supercooling ability), which is well documented with different kinds of insect pests: for example, European pine sawfly (Austarå, 1971), geometrid moths (Tenow and Nilssen, 1990; Ammunét *et al*., 2012) and aphids (Strathdee *et al*., 1995).

Outbreaking forest Lepidoptera tend to have their larval feeding period in spring on newly flushed foliage, and associated with that a disproportionately large number of them overwinter as eggs (Nothnagle and Schulz, 1987; Hunter, 1991). Virtanen and Neuvonen (1999b) analysed Finnish Macrolepidopteran species feeding on birch, aspen or willows, and showed that the proportion of species overwintering as larvae was highest in species with northern distribution type, while overwintering as adults or eggs was more common in species with southern distribution type. Despite this, the most prominent birch defoliators in northernmost Europe (autumnal and winter moths) overwinter as eggs (see Ammunét *et al*., Chapter 13, this volume).

Extreme cold is not the only challenge facing diapausing forest pests. In temperate and boreal climates, many insect species spend most of the year (often 9–10 months) in diapause, and too high temperatures during the inactive stage could exhaust their energy reserves (Hahn and Denlinger, 2007, 2011). Also, for species overwintering in the litter, the loss of snow cover or more numerous freeze–thaw cycles may be detrimental in a warmer climate (Bale and Hayward, 2010). Consequently, the effects of warming climate on the performance of overwintering insects are not universally positive. The net outcome will depend on the overwintering stage and site, and on the climatic zone considered.

Although winter is generally the unfavourable season in temperate forests, in some cases biotic factors (host-plant quality, natural enemies) can limit population growth during the summer so that the active life and population growth occurs in the cool season. Examples of this are the pine processionary moth (*Thaumetopoea pityocampa* Denis & Schiffermüller; see Battisti *et al*., 2005; Buffo *et al*., 2007; Netherer and Schopf, 2010) and anholocyclic aphids on conifers.

The green spruce aphid (*E. abietinum*) is a pest of *Picea* spp., and it causes most damage on Sitka spruce, *Picea sitchensis* (Bong) Carrière. It has spread widely and it occurs at least in central and north-west Europe, maritime north-west USA, New Zealand (Bejer-Petersen, 1962), and recently also in inland areas of south-west USA (Lynch, 2003, 2009). Green spruce aphid causes defoliation of economic importance, especially in maritime areas with mild winters, where the species overwinters mostly as apterous, viviparous females (Carter and Austarå, 1994), and can reproduce even at temperatures close to 0°C. In more continental areas (central Europe), the overwintering stage is egg (Bejer-Petersen, 1962), and aphid eggs have generally high cold-hardiness (Strathdee *et al*., 1995).

There are prominent seasonal patterns in the densities of green spruce aphids in oceanic Western Europe. The peak in density is generally in late May to early June (Day and Crute, 1990), after which the densities decline and remain low until August (Day *et al*., 2004). There is evidence that both declining host quality (amino acid concentration) and higher activity of natural enemies contribute to low aphid numbers in summer (Austarå *et al*., 1997; Day *et al*., 2004, 2006; Straw *et al*., 2009), and essentially limit the time available for positive population growth to the cooler parts of the year.

It has been suggested that the population growth of *E. abietinum* during winter and spring could be limited by weather via different mechanisms: (i) mortality due to cold temperatures (below –7°C); (ii) starvation and arrested development and population growth due to long periods with cool temperatures (below +5°C); and (iii) limited physiological time (degree days) before the decline in host quality in summer (Powell and Parry, 1976; Day and Crute, 1990).

Different authors specify different critical minimum winter temperatures for the survival of anholocyclic green spruce aphids. Furthermore, these can be modified by acclimation and the effects of feeding. For example, Carter (1972) found that newly born unfed aphids could survive at temperatures below –19°C, but a sudden drop of temperature to –11°C after an otherwise mild winter could check a potential spring outbreak of the green spruce aphid. Furthermore, in spring 1971, severe damage to *Picea* spp. was restricted to regions with minimum air temperatures >–8°C during the preceding winter (Carter, 1972). Microclimatic differences may also have an effect, as Powell and Parry (1976) recognized higher aphid survival in the lower branches, i.e. in the warmest part of the tree crown during the winter.

Bejer-Petersen (1962) found that the outbreak frequency of the green spruce aphid was higher in oceanic than in continental areas. He characterized the outbreak years in Denmark as years preceded by very mild winters (no monthly mean temperature below 0°C) and with an especially high monthly mean temperature for March. However, he notes that these monthly mean temperatures have little biological importance with respect to lethal temperatures. In a comparison of four anholocyclic populations (UK, Denmark, France, east Iceland) of green spruce aphid, Halldórsson *et al*. (2001) did not find differences between populations at potentially lethal temperatures: all populations showed 50% mortality at temperatures between –12°C and –14°C.

Lynch (2003, 2009) has found that *E. abietinum* causes severe damage to *Picea engelmannii* Parry and *Picea pungens* Engelm. in the mountains of interior south-west USA, in areas where winter temperatures fall well below the temperatures limiting aphid populations in maritime climates. She suggests that in this area the species has a holocyclic/paracyclic life cycle, and overwinters also as cold-hardy eggs. Aphid populations at damaging levels have been observed to survive at temperatures as low as –15°C (Lynch, 2009).

Low temperatures and other weather factors (e.g. strong winds) during the season with active life stages generally mean less time for feeding or flying activity (finding a mate, oviposition), and thus lower the realized fecundity and population growth rate (e.g. Persson, 1972; Kingsolver *et al*., 2011). On the other hand, during warm seasons, insect pests may be exposed to too warm or dry conditions. Kingsolver *et al*. (2011) have suggested that insects in both tropical and temperate regions have probably experienced increased mortality in response to high temperatures close to their upper thermal limits. The seriousness of these extremes depends on how well the active life stages (larvae and adults) can find shelter and/or adjust their diurnal activity pattern to avoid lethal extremes.

In temperate and boreal forests, several forest pests generally have only one generation per year. Increasing temperatures may allow multivoltinism in some species (e.g. *Ips typographus*, see Økland *et al*., Chapter 11, this volume), but not in all. Declining host quality constrains the possibility for a second generation in many defoliators overwintering as eggs and feeding on early-season foliage (Feeny, 1970; Kause *et al*., 1999). It has been suggested that lepidopteran species overwintering as pupae stage have the highest probability to increase the number of generations per year in a warming climate (Virtanen and Neuvonen, 1999b). During the past decades, increasing incidence of multivoltinism of moths has been observed both in central Europe and in boreal areas (Altermatt, 2010; Pöyry *et al*., 2011).

The number of generations does not, however, translate directly to increasing population growth rate. For example, in a South Korean population of *Dendrolimus spectabilis* Butler (Lepidoptera: Lasiocampidae), the fitness (as measured by size and fecundity) of the second generation was lower than that of the first generation (Choi *et al*., 2011; see also Roff, 1980). The population growth of the insect pest may also be sacrificed if there is time and warmth only for a partial second generation (see Økland *et al*., Chapter 11, this volume).

9.3 Outbreak Distribution and Frequency in Relation to Climatic Factors

To get at least a reasonably good idea of the distribution or frequency of forest insect outbreaks, the study period should be at least 30 years. Studies of this kind are, for obvious reasons, correlative in nature, and care is needed in the interpretation of the results. Table 9.1 shows some such studies focusing on defoliating pests. These and some related cases are discussed in more detail below.

The forest tent caterpillar (FTC), *Malacosoma disstria* Hbn., can cause complete defoliation of aspens in the Lake States of the USA and adjacent Canadian provinces (Witter, 1979). The most important abiotic factors affecting the collapse of the outbreaks have been suggested to be: (i) low winter temperatures causing high pharate larval mortality within the eggs; and (ii) harsh weather causing high larval mortality during the first 3 weeks after hatch; collapse can be caused also by food depletion or high pupal parasitism (Witter, 1979; Daniel and Myers, 1995, and references therein). The exact critical temperatures for winter egg survival may vary spatially and from year to year because of genetic differences and variation in the nature and duration of cold events (Witter, 1979; Cooke and Roland, 2003).

Daniel and Myers (1995) analysed visually the relationships between selected weather indices and FTC outbreaks in Ontario during a 41-year period. They did not find any clear relationship between temperatures during the larval feeding period and changes (increase versus decrease) in defoliation. However, they noticed that the outbreaks were most common in forested areas with mean overwintering temperatures over –40°C (Daniel and Myers, 1995). Cooke and Roland (2003) found higher FTC egg mortality in low-lying areas with cold-air pooling, and argued that cold winter

Table 9.1. Some cases where forest defoliator outbreak distribution or frequency have been studied in relation to climatic factors. See text for more details.

Pest insect[a]	Data type[b]	Period	Study area	Climate-related independent variables[c]	Response variables	Methods	Ref.[d]
FTC	DM	1948–1988	Ontario, Canada	Mean minimum overwintering T	Defoliation change; years of defoliation	Visual inspection of response variables plotted against independent variables	1
EPS	OR	1961–1990	Finland	Extreme minimum winter temperature	Proportion of outbreak years	Regression analysis	2
ESB	DM	1967–1998	Ontario, Canada	18 historic climatic variables	Defoliation frequency	CART[e]	3
ESB	DM	1941–1998	Eastern Canada	13 historic climatic variables	Outbreak duration, severity and constancy, etc.	Constrained ordination	4
ESB	DM	1967–1998	Ontario, Canada	Winter and summer mean daily min & max T, spring mean daily min T, summer mean P, monthly min & max T from May to August	Defoliation frequency	Random forests	5

Notes: [a]FTC = forest tent caterpillar; EPS = European pine sawfly; ESB = eastern spruce budworm; [b]DM = defoliation maps; OR = outbreak reports; [c]T = temperature; P = precipitation; [d]1 = Daniel and Myers (1995); 2 = Virtanen *et al.* (1996); 3 = Candau and Fleming (2005); 4 = Gray (2008); 5 = Candau and Fleming (2011); [e]CART = classification and regression tree.

temperatures were an important factor in FTC population dynamics in northern areas (cf. also Roland *et al*., 1998). On the other hand, Cooke *et al*. (2009), after analysing FTC defoliation records from Ontario and Quebec during a 65-year period (1938–2002), concluded that there did not appear to be any evidence that the range of FTC outbreaks in their study area was shifting gradually northward in response to a climate warming trend.

The European pine sawfly, *Neodiprion sertifer* (Geoffroy), is the most serious defoliator in the boreal pine forests of northern Europe (Juutinen and Varama, 1986). It overwinters in the canopy (the eggs are oviposited inside needles) and the eggs are killed at temperatures below –36°C (Austarå, 1971). In Finland, the outbreaks of this species occur at irregular intervals, and the incidence of outbreaks can be partially explained by soil type and minimum winter temperatures. The outbreaks during 1961–1990 were very rare in municipalities where the incidence of minimum winter temperatures below –36°C was over 37.5% (Virtanen *et al*., 1996).

The eastern spruce budworm (ESB), *Choristoneura fumiferana* (Clem.), is one of the most damaging insect pests in the coniferous forests of North America. In a classification and regression tree analysis of ESB defoliation frequency in Ontario, Candau and Fleming (2005) found that the lowest defoliation frequency was associated with lowest winter temperatures. An analysis of spruce budworm outbreak characteristics (duration, severity, consistency, lag) in relation to several environmental (climate, forest composition, spatial location) characteristics in eastern Canada illustrates, however, the complexity of interacting factors relevant in this system (Gray, 2008). In this study, the observed marginal effect of an increase in extreme minimum winter temperatures was to decrease the duration and severity of ESB outbreaks (Gray, 2008). Régnière *et al*. (2012) used an ecophysiological model to simulate the population dynamics of ESB. Their results suggest different relationships between ESB performance and temperature in different parts of the insect's range: at the southern edge of the distribution, high temperatures can cause exhaustion of energy reserves during diapause, while at the northern edge, cold temperatures can reduce overwintering survival (Régnière *et al*., 2012).

In addition to ESB, there are several related species/subspecies defoliating conifers in North America. Their distributions, host associations and relations to climate have been summarized by Volney and Fleming (2007). Western spruce budworm, *Choristoneura occidentalis* (Walsingham), outbreaks were recorded on southern Vancouver Island (British Columbia, Canada) in the early 20th century, but not after 1930, although outbreaks continued to occur in the interior regions of British Columbia. Increased winter temperatures affecting the timing of larval emergence more than the bud flush of the host trees, and consequently increasing the departure from optimal synchrony between larvae and high-quality host foliage, have been suggested as the main cause of this localized phenomenon (Thomson and Benton, 2007).

9.4 Spatial and Temporal Resolution Used When Analysing Forest Insect Pest Outbreaks

Long-term data about the distribution of forest pest outbreaks is often available only at coarse spatial resolution. Also, the spatial resolution of climatic data is generally rather low (Daly, 2006; Graae *et al*., 2012). On the other hand, the physiological and ecological processes that are behind these outbreaks function normally at smaller spatial scales. In their meta-analysis of the published literature on species distribution models, Potter *et al*. (2013) noted that there was huge spatial mismatch between organism size and the scale of climatic data: grid sizes of climatic data are about five orders of magnitude larger than the insects studied. The mismatch between the spatial and temporal scales of analysis and those of physiological and ecological processes is common also with forest insect pests (Table 9.2).

Table 9.2. Spatial and temporal resolution of data used in studying the relationships between climatic variables and forest insect pest outbreaks.

Pest insect[a]	Response variable[b]	Spatial resolution	Study area and spatial extent	Climatic variable(s), temporal resolution[c]	Ref.[d]
AM	EM	25 m×25 m grid	16 km×16 km in northern Finland	DMinT; 13–39 sites (data loggers); 3 winters; daily or seasonal (winter) resolution	1
FTC	EM	83 study plots, i.e. ~23 plots/100 km^2	Alberta, Canada; 360 km^2	DMinT from two meteorological stations	2
FTC	DM	100 km×100 km	Ontario, Canada	CA 1948–1988, from 20 weather stations	3
LBM	OTR	0.5°×0.5° grids	European Alps	MMT; MTP; winter (Dec, Jan, Feb) mean T	4
Bgeom	EM, SCP	0.25°×0.25° grid	Northern Fennoscandia	DMinT	5
ESB	DM	~17 km×~17 km grid	Eastern Canada ~1’423’000 km^2	13 simulated (BioSIM) climatic variables; seasonal (summer, winter) resolution	6
ESB	DM	1 km×1 km grid	Ontario, Canada	30-year (1961–1990) CNs of 18 climatic variables; seasonal (winter, spring, summer)	7
ESB	DM	10 km×10 km grid	Ontario, Canada	30-year (1961–1990) CNs	8
WSB	DM	2 km×2 km grid	Oregon, USA	30-year CNs of monthly means of DMaxT and DMinT and MTP	9
GM	DM	2 km×2 km grid	Pennsylvania, USA	30-year CNs of monthly means of DMaxT and DMinT and MTP	9

Notes: [a]AM = autumnal moth; FTC = forest tent caterpillar; LBM = larch bud moth; Bgeom = birch-feeding geometrids; ESB = eastern spruce budworm; WSB = western spruce budworm; GM = gypsy moth; [b]EM = egg mortality; DM = based on defoliation maps; OTR = outbreaks detected by tree-ring analysis; SCP = egg supercooling point; [c]DMinT = daily minimum temperatures; CA = climatic averages; MMT = monthly mean temperatures; MTP = monthly total precipitation; CN = climate normals; DMaxT = daily maximum temperatures; [d]1 = Virtanen *et al.* (1998); 2 = Cooke and Roland (2003); 3 = Daniel and Myers (1995); 4 = Johnson *et al.* (2010); 5 = Ammunét *et al.* (2012); 6 = Gray (2008); 7 = Candau and Fleming (2005); 8 = Candau and Fleming (2011); 9 = Williams and Liebhold (1995).

The outbreaks of the European pine sawfly have been rare in northern and eastern Finland, where winter minimum temperatures often go below the critical limit for egg survival (direct effect of temperature). In southern Finland, pine sawfly outbreaks were more common in areas with high frequency of dry soils (indirect effects of moisture availability via plant quality of pupal predation by small mammals). These patterns were statistically significant (Virtanen *et al.*, 1996) despite the large discrepancy between the spatial and temporal resolution between the outbreak records (annual records of outbreak occurrence at municipal level) and the physiological or ecological processes involved (Fig. 9.1).

Interpolated climate data for large regions are commonly available at various resolutions: e.g. from 0.25 degrees (~10–25 km) to 2.5 arcminutes (~4 km) to 30 arcseconds (~800 m) (see Hijmans *et al.*, 2005; Daly *et al.*, 2008; Mbogga *et al.*, 2009; Ammunét *et al.*, 2012; Aalto *et al.*, 2013). The precision and accuracy of these data depends on the climatic variable considered. Local stochastic weather patterns that may be relatively rare and variable from year to year (e.g. temperature inversions) can cause loss of precision in the data (Daly *et al.*, 2010). Daly (2006) states, ‘Spatial climate datasets represent a significant source of error in any analysis that uses them as input’, and gives guidelines for assessing the

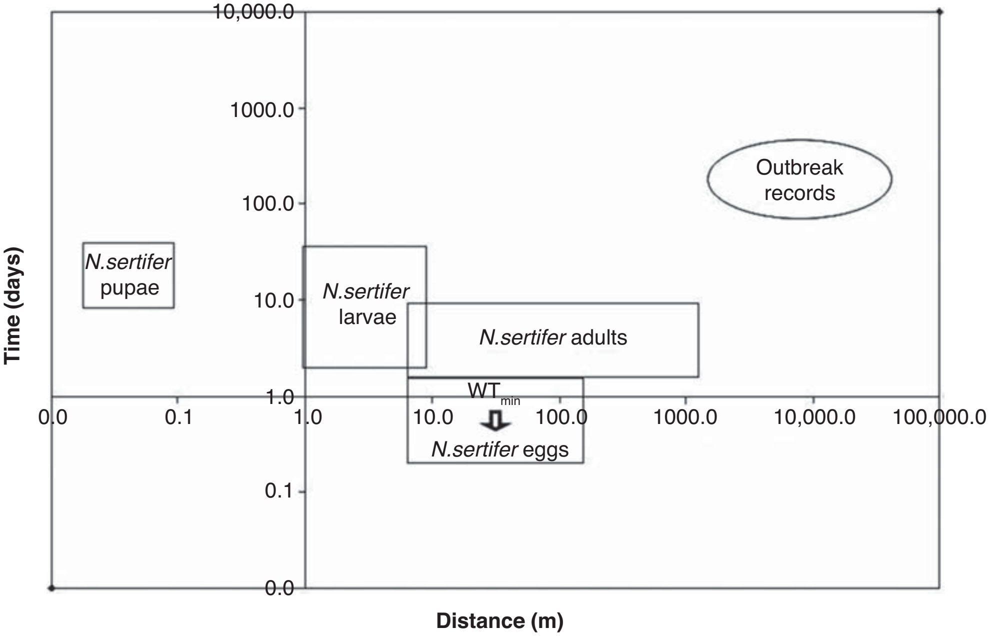


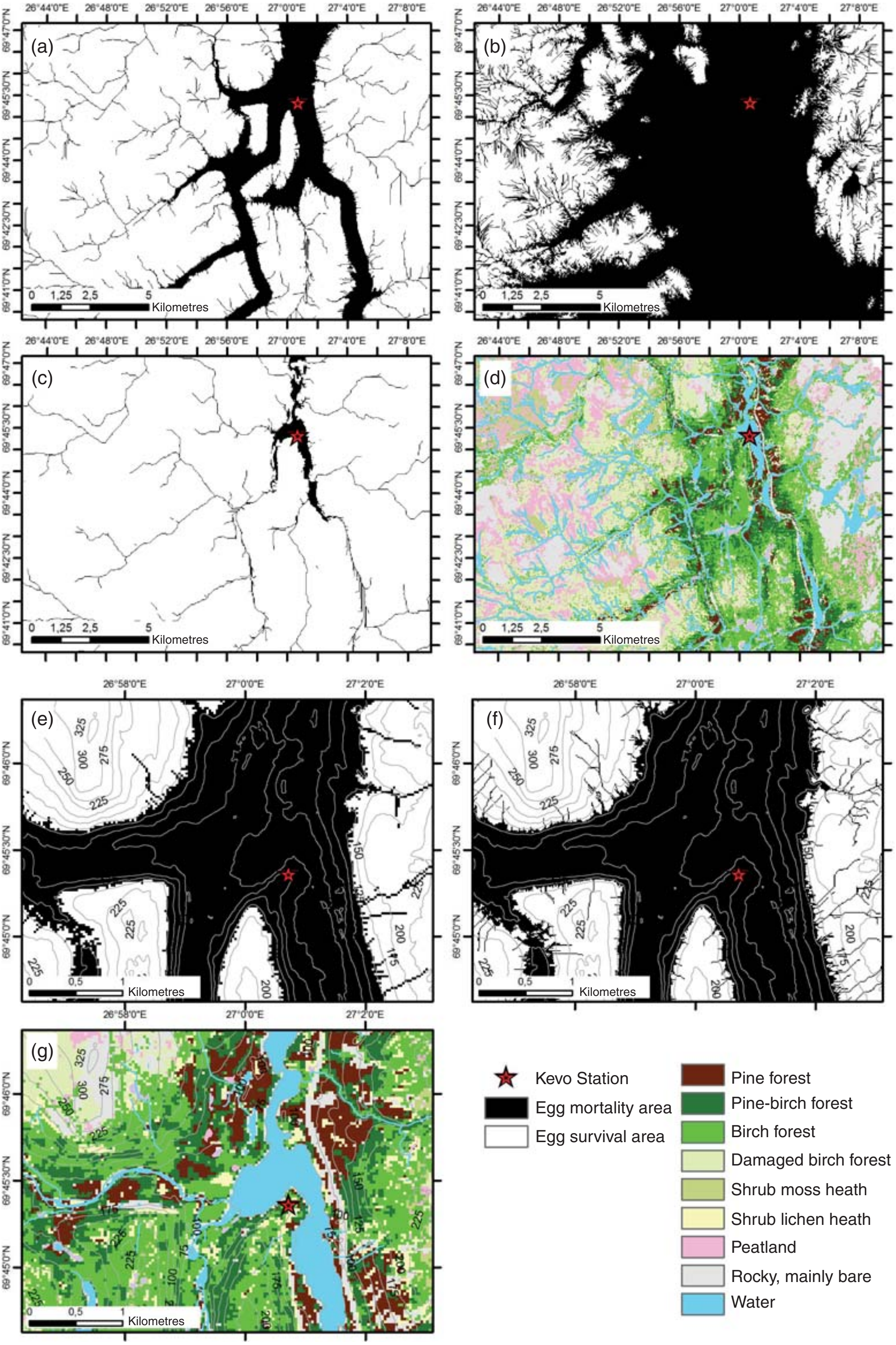
Fig. 9.1. Differences in spatial and temporal scales between the recording of outbreaks of the European pine sawfly (*Neodiprion sertifer*) and the physiological and ecological processes during different life stages: Overwintering eggs can be killed by even short exposures to winter temperatures (WT) below their supercooling point (–35°C); the interactions between larvae and host quality or natural enemies occur during early summer within the limited range of larval mobility; the practically sessile pupae of this species are exposed to predation for 1–2 months in summer; the adults fly in autumn and the females generally oviposit rather close to where they were born.

suitability of spatial climate data sets for different applications.

Topographically heterogeneous landscapes often show complex spatio-temporal variation in extreme minimum temperatures (e.g. Hogan and Ferrick, 1997; Virtanen *et al*., 1998; Lundquist *et al*., 2008; Suggitt *et al*., 2011). Large spatial temperature differences occur, especially during inversion situations in which radiatively cooled air drains into valleys and basins. Differences in minimum temperatures within 1 km can exceed 15°C during strong temperature inversions (Pepin *et al*., 2009). These inversions are strongest in winter (Pepin *et al*., 2009; Graae *et al*., 2012), but they can be important also during the warm season (Holden *et al*., 2011).

Figure 9.2 illustrates the spatial and temporal scales of variation in temperatures killing the eggs of the autumnal moth, *Epirrita autumnata* (Bkh.), in a 12 km × 17 km area in Finnish Lapland (calculations are based on models developed in Virtanen *et al*., 1998; the temperature data from the Kevo Meteorological Station comes from the Finnish Meteorological Institute). It is evident that a lot of spatial variation (both in egg mortality and vegetation types) is at scales below km^2, often at the scale of hectares. Estimating this variation is possible with targeted field campaigns that yield models linking the temperatures at meteorological stations with those in the surrounding topography (e.g. Virtanen *et al*., 1998; Lundquist *et al*., 2008).

Also, the annual variation in winter minimum temperatures in Kevo Meteorological Station (WTMinK) was extensive during the period 1962–2014: WTMinK ranged from –48.2°C to –31.8°C. The slope of WTMinK over time was 0.7°C/decade, i.e.


(a)
(b)
(c)
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(e)
(f)
(g)
26°44'0"E
26°48'0"E
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26°56'0"E
27°0'0"E
27°4'0"E
27°8'0"E
69°47'0"N
69°45'30"N
69°44'0"N
69°42'30"N
69°41'0"N
0 1,25 2,5 5 Kilometres
26°58'0"E
27°0'0"E
27°2'0"E
69°46'0"N
69°45'30"N
69°45'0"N
0 0,5 1 Kilometres
325
300
275
250
225
200
175
150
100
75
Kevo Station
Egg mortality area
Egg survival area
Pine forest
Pine-birch forest
Birch forest
Damaged birch forest
Shrub moss heath
Shrub lichen heath
Peatland
Rocky, mainly bare
Water

very modest when compared to interannual variation (the linear regression explained only 9.7% of the variation in WTMinK). The range of variation in WTMinK was also quite similar in the first and second half of the period (from –47.9°C to –33.9°C during 1962–1987 versus from –48.2°C to –31.8°C during 1988–2014). High interannual variation in temperatures is also common elsewhere: minimum winter temperatures in south-eastern USA varied by about 6–11°C/decade from 1960 onwards (Fig. 2 in Tran *et al*., 2007). This warns against making predictions based on only long-term (10–30 years) average temperatures.

Insect pests have complex life cycles, and different life stages living in different microhabitats can experience very different climatic conditions (e.g. Henson, 1958; Kingsolver *et al*., 2011). Many insects can also have adaptations to abiotic factors. For example, egg masses of the eastern tent caterpillar, *Malacosoma americanum* (Fab.), are covered by spumaline, which prevents desiccation and ameliorates low winter temperatures: in air temperatures below –10°C, the temperatures under the spumaline were on average 6°C higher than ambient temperatures (Segarra Carmona and Barbosa, 1983). Also, larvae of several forest pests build tents, which give shelter from adverse weather. Some pest larvae, like those of the gypsy moth, *Lymantria dispar* (L.), have insulating setae that reduce the rate of convective heat loss without affecting the capacity for radiant heat uptake, and the caterpillars can regulate their body temperatures behaviourally (at least up to +16°C above ambient temperatures) simply by changing orientation with respect to solar radiation (Casey and Hegel, 1981). Considering the variable responses of different life stages to changing climate and weather patterns is essential for understanding the impacts of global change on insect pests (Kingsolver *et al*., 2011).

The temperature excess of larval body temperature over the ambient temperature depends on the wind speed, radiation level and the position of the larval body in relation to radiant heat source. This temperature excess can vary from 2 to 16°C, giving considerable room for behavioural temperature regulation (e.g. Wellington, 1950; Shepherd, 1958; Casey and Hegel, 1981; Sears *et al*., 2011; Battisti *et al*., 2005, 2013). In topographically or structurally complex environments, the impacts of climate change could be ameliorated if the insects can move easily and choose microhabitats closer to their optimum temperatures (Sears *et al*., 2011).

Insects with sessile feeding stage (leaf/needle miners, gallers, borers) have limited or nil ability to behavioural thermoregulation. Daytime temperatures in mined leaves can be >10°C above the ambient temperatures, and there is considerable variation in leaf temperatures in different parts of the canopy (Pincebourde *et al*., 2007; Pincebourde and Woods, 2012; Saudreau *et al*., 2013). During extremely warm days, larvae in sun-exposed mines suffered from overheating, and consequently had increased mortality risk, while larvae in shaded mines had optimal conditions for development (Pincebourde *et al*., 2007).

Saudreau *et al*. (2013) developed a hierarchical simulation model environment for modelling leafminer body temperatures and mortality due to high summer (July) temperatures. Hourly body temperature dynamics, larval development and mortality were simulated for larvae dispersed in (virtual)

Fig. 9.2. *(opposite)* Areas of modelled egg mortality of the autumnal moth in the Kevo region, Utsjoki. (a) Egg mortality in a typical (median) winter for the period 1962–2014, digital elevation model used in 25 m pixel size, minimum temperature in Kevo Meterological Station (WTMinK) –38°C; (b) same as (a), but WTMinK –42°C (10% of winters were colder than this during 1962–2014); (c) same as (a), but WTMinK –32°C (= the warmest winter during 1962–2014); (d) vegetation and land cover types in the area of figures (a)–(c); (e) same as (a), but zoomed in to see more local landscape and with elevation contours; (f) same as (e), except digital elevation model used in 10 m pixel size; (g) vegetation and land cover types in the area of figures (e)–(f).

apple tree canopies. The results demonstrated convincingly the importance of using realistic (non-linear) rate curves and insect body temperatures rather than air temperatures in forecasting the impacts of climate change on pest outbreaks (Saudreau *et al*., 2013).

Considering that the microhabitat is also important during the winter season, Cooke and Roland (2003) found distinct differences in forest tent caterpillar egg mortality between vegetation strata: for example, after winter 1995/1996, the egg mortality was 20% in the aspen canopy, while it was 70% in the shrub layer. The probable explanation is that during temperature inversions the eggs on shrubs are exposed to colder temperatures, killing the eggs. As the proportion of FTC eggs laid on shrubs increases at high population densities, this introduces a temperature × population density interaction into the population dynamics of FTC, meaning that winter temperatures act in a partially density-dependent way (Cooke and Roland, 2003).

In their study of the role of minimum winter temperatures in the population dynamics of the southern pine beetle, *Dendroctonus frontalis* Zimm., Tran *et al*. (2007) developed a model predicting the phloem temperatures with an accuracy of ±1°C on the basis of air temperature and tree diameter. Beetles in trees were buffered by about 1–4°C from the lowest air temperatures.

Forest insect pests do not generally experience the weather and climatic conditions recorded at weather stations. Different interpolation methods and/or GIS techniques can be used when estimating the values of target variables in areas between the weather stations (e.g. Ninyerola *et al*., 2000; Daly, 2006; Aalto *et al*., 2013).

Although there are large differences in ambient temperatures between, for example, subtropical and boreal regions, the differences in growing season temperatures within the forest canopy (leaf temperatures) are clearly smaller, as boreal trees can have 5–15°C leaf temperature excess over the ambient temperature (Helliker and Richter, 2008; Pincebourde and Woods, 2012). New methods like infrared (IR) thermometry and micro loggers are available for obtaining high-resolution (both temporal and spatial) temperature data (Scherrer and Körner, 2010). IR images taken from a distance can cover rather large areas (several hectares) with about square metre resolution. However, one should remember that temperatures inside tree canopies differ from those of the outermost surfaces that are reflected in IR images (Scherrer and Körner, 2010).

9.5 Temporal Variation in Climate and the Population Dynamics of Forest Insect Pests

In temperate and boreal regions, interannual variation in climate is often very pronounced, and part of this variation is related to large-scale weather patterns. The North Atlantic Oscillation (NAO) is the leading pattern of weather (temperatures, winds, storminess, precipitation) variability in the areas surrounding the Atlantic. It refers to a north–south redistribution of atmospheric mass between the Arctic and the subtropical Atlantic. Table 9.3 shows some examples of studies on the population dynamics of forest insect pests in relation to the NAO or other climatic factors.

Commonly used NAO indices are based on atmospheric pressures in Iceland and the Azores/Lisbon/Gibraltar or on the principal component of sea level pressure anomalies over the Atlantic sector (Saldaña *et al*., 2007; Westgarth-Smith *et al*., 2007). However, there is no universally accepted index to describe the temporal variation in the NAO. Some indices show large within-season variance in the atmospheric circulation regimes and that most winters cannot be characterized solely by positive/negative NAO (Hurrell and Deser, 2009). Due to the ‘bipolar’ nature of the NAO, its effects differ between northern and southern areas. In the positive NAO phase, north-western Europe experiences higher winter precipitation and warmer temperatures (earlier spring), while southern Europe becomes drier (Meyers and Pagani, 2006; Westgarth-Smith *et al*., 2007).

Table 9.3. Examples of studies on the population dynamics of forest insect pests in relation to climatic factors.

Pest insect[a]	Host[b]	Data type[c]	Dependent variable[d]	Number of sites/areas	Years of data	Area[e]	Population dynamics model[f]	Explanatory (exogenous) variables[g]	Suggested mechanism of weather/climate effects	Ref.[h]
OA	Oak	STC	MJTC	8	26	Southern UK	Ricker (nl)	WT, WP	Winter precipitation increases the carrying capacity of the system	1
GSA	SS	AD	Residuals	1	8	NI	dd (linear)	Phys, freeze, chill	See below	2
GSA	SS	AD	APD	1	9	NI	dd (nl)	Phys, freeze, coma, rain	Negative effects of chilling bouts during winter and positive effects of thermal sum during spring	3
GSA	SS	STC	MCY	1	35	Scotland	dd (nl)			
GSA	SS	STC	TCY	1	41	GB	None	NAO (Oct–Mar); mean T (Oct–Apr)	Not specified	4
GSA	SS	STC	Rt(MCY)	9	32–40	GB	Ricker (nl)	Winter NAO; local weather (mean winter T; mean spring T)	Direct mortality effects due to freezing, and lower reproduction because of cold winters	5
GSA	SS	STC	MCY	15	20–22	GB	GAM (nl)	Winter NAO	Not specified	6
SPB	Pinus	IS	Rt(NIS)	1	39	Eastern Texas, USA	Cubic direct and delayed dd	NHD, MWT (quadratic) + interactions with dd factors	NHD <=> upper lethal temperatures exceeded; MWT <=> mortality at low MWT, reduced population growth rate at high MWT	7
SPB	Pinus	TC	Rt(PTC)	140	17	South-eastern USA	dd and ddd	MWT (phloem)	Winter mortality	8

Notes: [a]OA = oak aphid; GSA = green spruce aphid; SPB = southern pine beetle; [b]SS = sitka spruce; [c]STC = suction trap catches; AD = aphid density on trees; IS = number of infestation spots; TC = trap catches; [d]MJTC = May–July total catch, adj. with oak density per county; APD = annual peak (May/June) density; MCY = max catch per year; TCY = total catch per year; NIS = number of infestation 'spots'; PTC = pheromone trap catch; [e]NI = Northern Ireland; GB = Great Britain; [f]nl = non-linear; dd = density dependence; ddd = delayed density dependence; [g]WT = winter temperature; WP = winter precipitation; NAO = North Atlantic Oscillation; T = temperature; NHD = number of hot days; MWT = minimum winter temperature; [h]1 = Estay *et al.* (2009); 2 = Day and Crute (1990); 3 = Day *et al.* (2010); 4 = Westgarth-Smith *et al.* (2007); 5 = Lima *et al.* (2008); 6 = Saldaña *et al.* (2007); 7 = Friedenberg *et al.* (2008); 8 = Tran *et al.* (2007).

Large-scale climate indices (e.g. the NAO) have been found, rather paradoxically, to perform better than local weather variables (e.g. monthly mean or minimum temperatures, monthly precipitation) in explaining climate-related variability in the performance or population dynamics of animals. Hallett *et al*. (2004) and Stenseth and Mysterud (2005) formulate the probable reasons for this: (i) the exact timing of a critical weather event can vary by several months from year to year, and consequently, large-scale climate indices spanning several months can represent this variation better than monthly weather variables; (ii) the exact type of critical weather event can also differ from year to year, with similar consequences because, for example, of the NAO variation in several variables (temperatures, precipitation, wind speed, etc.); (iii) in spatially heterogeneous environments, the effect of the NAO can vary geographically (the spatial window component of the NAO, *sensu* Stenseth and Mysterud, 2005). It is probable that the NAO and corresponding indices reflect only incompletely the complicated associations between local weather and ecological processes, and given sufficient knowledge of the relevant processes should enable the construction of better working 'weather packages' for specific cases (Hallett *et al*., 2004; Stenseth and Mysterud, 2005).

Westgarth-Smith *et al*. (2007) found that the temporal variations in the suction-trap catches of the green spruce aphid (*E. abietinum*) in Rothamsted (UK) had significant positive correlations with the October–March NAO index ($R^2 = 24\%$) and with the mean October–April temperature ($R^2 = 27\%$). Saldaña *et al*. (2007) analysed the spatio-temporal dynamics of *E. abietinum* in Great Britain with a non-parametric regression approach, having past aphid catches and a winter (December–March) NAO index as explanatory variables. Eleven of the 15 time series (locations) they analysed showed significantly positive NAO effects, indicating that mild and wet winters had positive effects on per capita growth rates of aphids. In most cases, the NAO effect was clearly non-linear, with strong negative effects at low NAO values (Saldaña *et al*., 2007). The population dynamics of *E. abietinum* show a high level of spatial synchrony up to about 350–400 km for those populations affected by the NAO (Saldaña *et al*., 2007).

Hodar *et al*. (2012) studied the relationships between the winter NAO index and pine defoliation by pine processionary moth larvae in Spain over 18 years (1992–2009). They found rather weak (with all pine species R^2 varied from 1 to 13%; cf. their Fig. 1) and complex relationships between the NAO and the percentage of stands having at least strong defoliation in some part of the stand, depending on which pine species was involved and the time lag associated with the suspected NAO effect (from the current to the three previous winters). The problem with this analysis might have been that Hodar *et al*. (2012) used the incidence of pine stands with defoliation as the response variable, while from the perspective of population dynamics it would have been more informative to use changes in defoliation incidence as the response. Our reanalysis of their data (from Table 1) showed that the winter NAO of year t-1 explained 32% of the variation in the logarithm of the change in defoliation incidence from year t-1 to year t (for all stands; for stands with full time series $R^2 = 37\%$).

Day *et al*. (2010) analysed the interannual dynamics of aerial and arboreal *E. abietinum* populations in the northern UK, and they constructed a model that could be applied to both kinds of data. This model had a log-linear directly density-dependent term and two climatic variables: *coma* (= number of chill days (daily mean temperature ≤ 5°C) throughout the previous winter) and *phys.adj* (= physiological/thermal time (degree days above +4°C) accumulated from 1 January to 30 April, and adjusted to the average for the site). Per capita growth rates were associated negatively with winter cold (*coma*) and positively with spring warmth (*phys*). These results also provide confirmation that alate populations of spruce aphids (estimated by suction-trap catches) are a reasonable proxy for aphids on trees (Day *et al*., 2010).

Estay *et al*. (2009) analysed annual suction-trap catches (26 years; from 1980 to

2006) of the oak aphid, *Tuberculatus annulatus* (Hartig), at eight sites in the UK. They modelled the endogenous forces (intraspecific competition) with Ricker's equation, and used average winter temperatures and total winter precipitation as potential exogenous explanatory variables. Their results suggested that in four of the eight aphid populations studied, winter precipitation affected the population dynamics by modifying the carrying capacity. Furthermore, a path analysis showed that the synchrony in population dynamics was highly correlated with synchrony in winter precipitation (Estay *et al*., 2009).

Friedenberg *et al*. (2008) analysed the role of density-dependent (endogenous) and climatic (exogenous) factors in the population dynamics (annual numbers of infestation 'spots') of the southern pine beetle (*D. frontalis*) in eastern Texas. They compared four different models of density dependence with and without climatic covariates. The model that performed best had cubic direct and delayed density dependence (i.e. the model has low and high stable equilibria and an unstable threshold between them), together with two climatic variables (number of hot days (NHD) – linear negative effect; minimum winter temperature – with negative quadratic term) and a quadratic interaction between NHD and delayed density dependence. Summarizing, the model predicted declining population growth with higher numbers of days exceeding +32°C and highest population growth with average minimum winter temperatures. Furthermore, the form of density dependence changed with NHD.

9.6 Predicting the Effects of Changing Abiotic Factors on Forest Insect Outbreaks

The examples reviewed above show the potential complexity of the relationships between climatic factors and the population dynamics of forest pests. Clearly, more research with long-term data sets is needed to develop a more comprehensive understanding of these relationships, even for the most economically important forest insect pests.

Insect physiologists and ecologists warn against making unwarranted generalizations about the effects of future climate change on the frequency or intensity of forest insect outbreaks (e.g. Hahn and Denlinger, 2007; Hance *et al*., 2007; Bale and Hayward, 2010; Kingsolver *et al*., 2011). The research literature is probably biased in favour of pest species where positive responses to increasing temperatures could be expected, as the study objects are not generally randomly selected. A rare exception (also due to its length – 61 years) is the study by Moraal and Jagers op Akkerhuis (2011), in which 98 of the most common pests on trees in the Netherlands were included in the study. Of the species studied, 27 showed a decline and 31 showed an increase during 1946–2006 (winter temperatures increased by 2°C during this period), while the rest did not show any obvious trend or had infestation lasting only a few years (Moraal and Jagers op Akkerhuis, 2011). Obviously, the species respond to environmental changes more or less individualistically, and in addition to climate, land use and forest management practices also change during such long periods and affect the probability of pest outbreaks (cf. also Hunter *et al*., 2014).

Another issue is the great uncertainty about how regional climates change in the future. Although there is apparently a consensus about a globally warmer future, the local and regional climates are relevant for predicting the changes in forest insect pest outbreaks, but there is huge variation in the outcomes from different climate models. A study comparing the effects of modelling climate change, with projections from three global circulation models (GCMs) on the simulated (on the basis of degree days) numbers of generations in several Californian insect pests (including six species on fruit trees), revealed that the choice of CGM explained a considerable proportion of the variation in voltinism, more than, for example, geographical location or period (cf. also Jönsson and Bärring, 2011; Ziter *et al*., 2012).

The effects of changes in specific abiotic factors on forest insect populations depend on the pest species and region under consideration, and these effects can even be opposite. For example, an increase in winter temperatures can increase the area susceptible to outbreaks of birch-feeding geometrids (see Ammunét *et al*., Chapter 13, this volume) and the European pine sawfly (Virtanen *et al*., 1996) in northern Europe. On the other hand, increasing winter temperatures have been suggested as the main cause of the collapse of larch bud moth cycles in the Alps (Baltensweiler, 1993; Esper *et al*., 2007; Johnson *et al*., 2010).

Researchers studying even a single system have reached divergent conclusions about the expected impacts of climate change on insect outbreaks. For example, Régnière *et al*. (2012) used ecophysiological modelling to simulate the climatic responses of the spruce budworm and said: 'Our work concludes that the extent of spruce budworm outbreaks in the eastern portion of its North American range should decrease in response to climate change, while a correlative study by Gray (2008) suggests just the opposite'. A further example comes from changes in phenology that may affect the synchrony between pest and the host plant and natural enemies (Visser and Holleman, 2001; Bale and Hayward, 2010). The role of possible asynchrony in modulating, for example, spruce budworm outbreaks is complex and its impacts hard to evaluate, as shown by the conflicting conclusions of Volney and Fleming (2007) versus Candau and Fleming (2011).

9.7 Conclusions

As discussed above and elsewhere (e.g. Dukes *et al*., 2009), the relationships between variable and changing climate and the population dynamics of forest insects are rarely straightforward. Furthermore, climate models are typically constructed to predict average conditions well, but rare extreme events can be even more important for forest pest abundance. Thus, multidisciplinary cooperation between researchers in different fields (e.g. entomologists, forest ecologists, GIS experts, climatologists, micrometeorologists, statisticians, modellers, engineers) is urgently needed when trying to bridge the gap between the scales of insect pests and climate models and data (Lawton, 1994; Potter *et al*., 2013). This is a necessary step in the understanding and modelling of the impacts of variable and changing climate on forest insect pests.

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10

Responses of Tree-killing Bark Beetles to a Changing Climate

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Abstract

Bark beetles cause widespread tree mortality, so understanding how climate change will influence the distribution and magnitude of outbreaks by this group of herbivores is important. We first develop a framework of outbreak dynamics that emphasizes transitions from states dominated by negative feedback to those dominated by positive, density-dependent feedback. We then consider mechanisms by which temperature and precipitation changes can allow populations to breach critical thresholds, and the empirical data relating outbreaks to weather. Finally, we consider how anticipated climatic change, and relationships with new hosts and natural enemy guilds, may influence dynamics in new habitats. There is strong evidence that elevated temperature can increase overwintering survival and decrease generation times of bark beetles, although evolved traits can also constrain response to warming in some habitats. Moreover, combinations of phenotypic plasticity, genotypic variation and physiological thresholds yield a broad range of conditions under which adults emerge synchronously, and thus can mass attack trees. There is likewise strong evidence that severe drought reduces tree defences against attack. Drought stress can occur through lower precipitation and/or higher temperatures that reduce soil moisture and/or raise vapour pressure deficit. We also delineate three categories of range modifications: increased and more persistent establishment in areas where trees experienced only intermittent exposure historically; establishment in areas dominated by host species but where local populations experienced little or no pressure historically; and movement into new areas containing susceptible species that have not been exposed previously. Each of these has been documented for bark beetles. Trees in areas that experienced minor or no exposure generally had lower defences than their more historically exposed counterparts. However, there can be lags in beetle

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behavioural responses. In some cases, more heterogeneous forest structure, more abundant local predators and competitors and low host nutritional quality could potentially lessen risk in new habitats. Direct comparative studies are needed to evaluate outbreak potentials following range expansions driven by climate warming.

10.1 Introduction

Understanding how bark beetles respond to changing temperature and precipitation regimes can be particularly useful for several reasons. First, these insects inhabit both natural and managed ecosystems and exert both environmental costs and benefits. Second, bark beetles include several historically eruptive species that undergo natural outbreaks, thereby providing opportunities to evaluate both potential changes in historical outbreak dynamics and novel dynamics in new habitats. Third, their behaviours can exert positive feedbacks on population dynamics at organismal and stand levels that translate into non-linear dynamics at higher levels. This is particularly relevant to our understanding and projections of climate-driven tipping points. Fourth, these insects affect fundamental ecological processes and exert major influences on the landscapes in which they reside. Fifth, bark beetles have close symbiotic associations with fungi and bacteria, as well as strong antagonistic interactions with some microbes. Each of these microorganisms undergoes its own responses to temperature and moisture conditions, so understanding these systems can improve our ability to project how species complexes and communities will react to climate change. Sixth, several bark beetle species are already showing both altered outbreak dynamics within their historical ranges and expanded geographic and host ranges, in response to changing climate. This allows us to incorporate both mechanistic and empirical modelling approaches into future projections. Here, we integrate existing knowledge on bark beetles in North American conifer forests with projected temperature and precipitation regimes, to assess how these systems may respond to climate change.

10.2 Ecology and Population Dynamics of Bark Beetles: The Template on which Responses to Anthropogenic Change Occur

10.2.1 Ecological roles and generalized life history of bark beetles

Bark beetles (Curculionidae: Scolytinae) contain a high diversity of life histories, host-plant associations, geographic ranges, ecological roles and symbiotic relationships. Most species cause little to no negative economic impacts, and provide environmental benefits such as nutrient cycling, gap formation and nutrition for wildlife. The overwhelming majority of species in native systems are associated with dead or dying trees, or dead tissues of live trees (Lindgren and Raffa, 2013). A much smaller proportion can sometimes kill trees. Populations of a small subset of tree-killing species intermittently rise to sufficiently high levels to both cause socio-economic losses and function as landscape-scale disturbance agents. The tree-killing and outbreaking species are almost entirely colonizers of the main stems of conifers, primarily in the genera *Dendroctonus*, *Ips* and *Scolytus*. We focus primarily on these groups in North American conifers.

Bark beetles spend most of their lives in host plants. Adults emerge from the trees in which they developed, fly, land in response to visual and olfactory stimuli, and use host chemical and tactile cues to determine whether to enter a tree or resume flight. They tunnel through the bark into the phloem and produce aggregation pheromones that attract both mates and additional members of the same sex. These pheromones are complex mixtures and are closely linked to tree physiology. Many species exploit host monoterpenes as precursors and/or synergists of their pheromones (Wood, 1982). Females construct galleries along which they oviposit, and the larvae feed on phloem and fungi. The brood pupate, undergo a brief teneral adult stage and emerge as adults. Because bark beetles and their microbial associates develop in tissues critical to plant nutrient and water transport, successful development typically results in tree death. This has two important ramifications to their population dynamics. First, the mortality they cause has placed strong selective pressures on trees to evolve complex, multi-component defence systems. Second, the tree is usually an available resource for only one beetle generation, so each cohort must locate and colonize new trees. Generation times vary with species, latitude and weather, ranging from multiple generations per year in *Dendroctonus frontalis* Zimmermann to one generation every several years in *Dendroctonus ponderosae* Hopkins at its range limits. Within a given locale, and across latitudes, a single species can exhibit plasticity in temperature-dependent voltinism (Hansen *et al*., 2001; Bentz *et al*., 2011).

Bark beetles are closely associated with a broad range of microorganisms. Typically, one or two ophiostomatoid fungi are associated with each beetle species. Their roles vary among systems. Some fungi benefit larval nutrition (Bleiker and Six, 2007), others are antagonistic and some have context-dependent relationships (Klepzig *et al*., 2009). Some fungi appear capable of killing trees or degrading host toxins (Lee *et al*., 2006; Diguistini *et al*., 2011; Hammerbacher *et al*., 2013), but the extent to which they do so is under debate (Lieutier *et al*., 2009; Six and Wingfield, 2011). The composition of fungal associates can vary with temperature (Six, 2003; Addison *et al*., 2013), beetle population phase (Aukema *et al*., 2005) and other factors. Bacteria (Brand *et al*., 1975; Scott *et al*., 2008; Morales-Jimenez *et al*., 2012; Boone *et al*., 2013) and yeasts (Davis and Hofstetter, 2011) may likewise contribute to nutritional exploitation of the substrate, reduction of chemical defences, protection from antagonists and possibly pheromone synthesis. Bacteria vary among bark beetle species, hosts and populations (Adams *et al*., 2010, 2013a).

10.2.2 Population dynamics

Populations of tree-killing bark beetles undergo dramatic fluctuations. Within a given region, abundances remain low and relatively stable for lengthy periods, varying with minor changes in resource availability, weather and predisposing biotic agents. During these periods, beetles are limited to highly stressed trees, which pose relatively little resistance but are ephemeral in space and time, often provide relatively low nutritional value and are available to many competing species (Safranyik and Carroll, 2006). Under certain conditions, however, populations rise suddenly, spread over large areas and kill enormous numbers of previously healthy trees.

In systems with such bimodal behaviour, understanding how populations can transform from a state dominated by negative feedback to one of net positive feedback can suggest how changing climate may alter dynamics. Four major components are important for bark beetles (Fig. 10.1) (Raffa *et al*., 2008). First, a stand must have the appropriate host species and age structure. Most tree-killing bark beetles are confined to one or sometimes two tree genera. Beetles are further limited to mature trees that are large enough to support broods within their phloem. Stands that have low species and age diversity, are dense and are old are more likely to experience outbreaks (Safranyik and Carroll, 2006).

Second, conifers are equipped with multi-component integrated defences that can resist attack by beetle–microbial complexes, but these are highly sensitive to environmental stress. Conifer defences include physical features such as bark toughness and resin flow (Raffa and Berryman, 1983; Kane and Kolb, 2010), histological defences such as autonecrosis and traumatic duct formation (Franceschi *et al*., 2005; Schmidt *et al*., 2011), and chemical defences such as monoterpenes, diterpene acids, phenylpropanoids and phenolics (Klepzig *et al*., 1996; Kelsey *et al*., 2001; Faccoli and Schlyter, 2007; Manning and Reid, 2013). These modalities are highly integrated. For example, resin acts as both a physical barrier and a matrix of

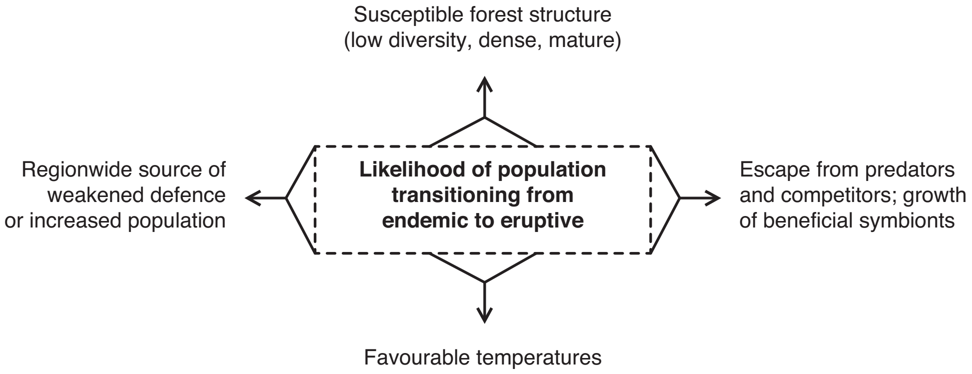

Fig. 10.1. Conceptual diagram of non-mutually exclusive climatic, landscape and trophic factors that increase individually or jointly the likelihood of bark beetle outbreak. Conditions are typically inadequate for beetles to overcome constraints on population growth, and only a narrow set of conditions allows populations to pass through an 'eruptive window'. Beyond this threshold, beetles generate substantial positive feedback, and lower-scale constraints commonly exert less effect. Each of the factors shown can reduce the corresponding constraint, increasing that portion of the portal. The relative importance of each factor in transitioning from endemic to eruptive dynamics varies among systems.

toxins, structures such as resin ducts and glands provide conduits for delivering allelochemicals, and autonecrosis confronts beetles with physical suberization, localized toxin accumulation and nutrient starvation. Both physical and chemical defences can be constitutive or induced (Franceschi *et al.*, 2005). Induced resinosis can inhibit attraction to pheromones produced by entering beetles (Erbilgin *et al.*, 2006). Induced chemical responses include increasing concentrations from tolerable to toxic levels, changing relative abundances, often with disproportionately high biosynthesis of the more toxic compounds, and producing new compounds not detectable in constitutive tissue (Huber *et al.*, 2004; Raffa *et al.*, 2005; Keeling and Bohlmann, 2006). A wide variety of biotic and abiotic stresses have been shown to reduce tree defences and increase the incidence of attack (Lombardero *et al.*, 2000b; Boone *et al.*, 2011; Hart *et al.*, 2014).

Third, temperature both imposes severe limitations on beetles' geographic ranges and is an important driver of their abundance (Trân *et al.*, 2007; Powell and Bentz, 2009). Temperature influences voltinism, within-generation synchrony and seasonality, and ultimately survival. Interactions between temperature and developmental parameters can be particularly critical in some tree-killing bark beetles because synchronous emergence can foster their ability to overcome tree defences jointly (Bentz *et al.*, 1991).

Fourth, predators and competitors play important roles. Predators, such as woodpeckers, beetles and flies can exert high mortality (Schroeder and Weslien, 1994; Turchin *et al.*, 1999). Several parasitic insects attack bark beetles, but they typically cause less mortality than to other herbivore guilds, due to protection by bark. Competitors often exert high costs on beetle reproduction (Reeve *et al.*, 1998). The predominant competitors are other bark beetles and wood borers, often those that specialize on dead or highly stressed trees. Competition can arise from moderately aggressive species exploiting a common stressed-tree resource, or from a diverse guild of saprophages exploiting trees killed by primary bark beetles. Alongside these trophic interactions, particular assemblages of symbionts can strongly influence beetle reproduction (Bleiker and Six, 2007; Hofstetter *et al.*, 2007).

Several features of the conditions required for transition from endemic to eruptive dynamics are pertinent to climate change. First, the drivers and constraints (Fig. 10.1) interact. For example, warming temperature can benefit beetles directly, but also influences the composition of symbionts (Addison *et al*., 2013) and stresses trees through lower soil moisture and higher vapour pressure deficit. Likewise, the importance of interspecific competition depends on population phase; specifically, whether beetles are restricted to stressed trees or extend into healthy trees (Powell *et al*., 2012). Second, these processes operate across scales. For example, the efficacy of individual tree defence is influenced by higher-scale factors such as forest structure, weather and long-distance dispersal of attacking beetles (Simard *et al*., 2012). Third, once conditions allow populations to rise past the eruptive threshold, positive feedback can persist even after the eliciting driver has been relaxed. Fourth, single drivers are often insufficient to carry populations past the eruptive threshold, despite their individual importance. For example, when temperatures in coastal Alaska are warm and dry enough for *Dendroctonus rufipennis* to transition from semivoltine to univoltine development, outbreaks become likely (Werner and Holsten, 1985; Berg *et al*., 2006; Sherriff *et al*., 2011). Yet outbreaks are rare among the univoltine *D. rufipennis* populations of interior Alaska and the Great Lakes region, probably because of a combination of dry conditions that favour competitors and cold winters in Alaska and forest heterogeneity and natural enemies in the Great Lakes region (Haberkern *et al*., 2002; Werner *et al*., 2006).

When anticipating the effects of climate change, it is helpful to recognize there are precedents for other anthropogenic activities raising innocuous bark beetle–microbial complexes to severe pest status. The most dramatic cases arose when beetle–fungal complexes were introduced by humans into areas in which native trees had not co-evolved and host resistance was lacking (Gibbs, 1978; Sun *et al*., 2013). Other examples include habitat manipulations that yielded more susceptible, homogeneous forest structures (Jactel and Brockerhoff, 2007) and fragmentation that directly benefited bark beetles or reduced prey tracking by predators (Coulson *et al*., 1999; Ryall and Fahrig, 2005).

10.3 Effects of Climate Change on the Frequency and Severity of Outbreaks

Attributing unusually large outbreaks to human-caused climate change requires several conditions. First, temperature and precipitation changes need to be related to human activities, which is well established in many analyses (IPCC, 2007; Barnett *et al*., 2008). Second, the frequency and severity of outbreaks need to be correlated with climatic changes, which has been shown both within historical ranges (Berg *et al*., 2006; Logan and Powell, 2009; Sherriff *et al*., 2011; Creeden *et al*., 2014), and northward and elevational expansions (Carroll *et al*., 2004; Logan *et al*., 2010; Sambaraju *et al*., 2012; Weed *et al*., 2013) by several species. Third, association of outbreaks with climatic variables is most compelling when it can be linked mechanistically to processes known to affect insect development, behaviour and reproduction. The direct and indirect effects of temperature (Section 10.3.1) and drought (Section 10.3.2) on multiple features of bark beetle performance are quite pronounced, and are becoming increasingly understood.

10.3.1 Effects of temperature on bark beetle synchronicity, seasonality and survival

Temperature is a significant driver of bark beetle life history traits that promote synchrony of vulnerable life stages with appropriate seasons (i.e. seasonality) and tolerance of adverse environmental conditions. For those species that require coordinated attacks to overcome tree defences, temperature can further influence population success through the synchronous emergence of adults (Logan and Bentz, 1999). Many physiological processes throughout multiple life stages can influence synchrony, seasonality and survival (Table 10.1), including: (i) thermal thresholds and rates of development; (ii) diapause; and (iii) cold hardening. Because these temperature-dependent traits are shaped by natural selection to provide optimal fitness in a given environment, they vary among and within species that are distributed across large climatic ranges. Climate change will directly influence bark beetle populations through these traits.

Developmental thresholds and rates

Low and high thresholds bound the thermal range for insect development and are important factors in population survival and growth that vary among and within species (Deutsch *et al*., 2008). Examining low and high temperature thresholds is complicated, however, by non-linearities that influence survival at temperature extremes (Régnière *et al*., 2012). Low thermal thresholds for development can be important population synchronizing factors when they differ among life stages, particularly in species that live in cool habitats (Bentz *et al*., 1991). When development in older life stages (i.e. prepupae) only occurs at high temperatures, yet development in younger life stages (i.e. eggs and early instars) can occur at low temperatures, development is halted in older individuals while continuing in younger ones as temperatures cool. Later-hatching individuals can 'catch up' with those oviposited first, promoting synchronization of life stages across a population (Bentz *et al*., 1991). High thermal thresholds for development and temperatures that result in the fastest development are also important, yet unknown for most bark beetle species. Optimal development rates are between 27 and 30°C for *D. frontalis* (Wagner *et al*., 1983), and near 28°C for *Dendroctonus simplex* (McKee and Aukema, 2015a), yet *D. ponderosae* development declines above 25°C (Régnière *et al*., 2012). A rise in development rate with increasing temperature up to some maximum, followed by a rapid decline, is common in insects, and has important implications for population response in a warming climate. Species already living at or near their thermal maximum (i.e. small 'thermal safety margin') may be more impacted by climate warming as temperatures exceed optimal thresholds, especially those with sharp declines in development rate at temperatures above the optimum. Populations in cooler environments typically have thermal optima higher than their current environment (i.e. large 'thermal safety margin') relative to populations in warmer environments (Deutsch *et al*., 2008), and therefore initially respond positively to warming temperatures. For example, at many cool, high-elevation sites, recent temperature increases remain in the thermal range of increasing development rate for *D. ponderosae*, resulting in a decrease in generation time. At warm, low-elevation sites, however, historical temperatures were already at or near the threshold for optimal development and increased warming has had little effect on generation time (Bentz *et al*., 2014).

Although warming temperatures can shorten the generation time of some individuals (Werner and Holsten, 1985; Hansen *et al*., 2001; Bentz *et al*., 2014), evolved development rates and thresholds limit where and how fast this occurs. For example, although *D. ponderosae* may complete a generation in a single summer when temperatures are warm and attacks occur early (DeLeon *et al*., 1934; Bentz *et al*., 2014), few adults are typically present in early summer, and development rates and thresholds limit the capacity to produce a second generation across winter (Bentz and Powell, 2014). The complexity of bark beetle temperature-dependent physiology that has evolved to promote population success across varying environments complicates predictions of response to future climatic conditions. New thermal regimes in some habitats may reduce outbreaks of some species, yet changes in other habitats may favour them. A detailed understanding of development rates, thresholds and diapause will be required to make useful predictions.

Diapause

Diapause is the most common strategy by which insects gain protection from regular periods of adverse environmental

Table 10.1. Temperature-dependent life history parameters that can influence response to climate change and contribute to phenotypic plasticity and heritable variation in bark beetles.

Parameter	Definition	Relationship among bark beetles	Ecological significance	References
Development rate	Rate for completion of a life stage	Development rate shows a parabolic relationship with temperature, increasing from T_{min} to T_{opt}, then dropping rapidly to T_{max}. Can vary among life stages within a species and among species	Influences seasonality and voltinism	1, 9, 12, 15, 18, 22, 23
Optimal developmental threshold T_{opt}	Temperature at which insects experience most rapid development	Varies among species	Populations currently living in environments that are on average cooler than their T_{opt} can respond to climate warming with increased development and potentially decreased generation time	1, 9, 15, 18, 22, 23
Maximum developmental threshold T_{max}	Temperature above which development ceases	Varies among species	Populations living in warm environments may approach T_{max} faster with climate warming than those in cool environments	1, 9, 15, 18, 22, 23
Minimum developmental threshold T_{min}	Lowest temperature at which development continues	Often higher in later life stages than early life stages	Differences among life stages can promote seasonality and adult emergence synchrony	1, 9, 15, 18, 23
Diapause, facultative	Dormancy elicited by environmental cues	Prepupal and adult dormancies in many species	Promotes seasonality and dictates the number of generations per year. Increased probability of being averted with climate warming, resulting in reduced generation time	3, 4, 6, 8, 9, 10, 12, 13, 16, 21
Diapause, obligate	Dormancy that is a requisite component of life history	Adult reproductive dormancy in several species	Promotes seasonality and synchrony of adult emergence	5, 12, 19, 20
Cold hardening	Accumulation of cryoprotectant compounds to reduce supercooling point (SCP), the temperature at which mortality occurs	Freeze intolerance is universal among species. SCPs vary seasonally and among and within species	Species that overwinter under bark have lower SCPs than those that overwinter in soil. SCPs vary seasonally in cold relative to warm habitats. Soil inhabiting species may be affected negatively by reduced snowpack	2, 7, 11, 14, 17

Notes: [1]Bentz *et al*. (1991); [2]Bentz and Mullins (1999); [3]Birch (1974); [4]Christiansen (1971); [5]Clark (1974); [6]Doležal and Sehnal (2007); [7]Gehrken (1984); [8]Gehrken (1985); [9]Hansen *et al*. (2001); [10]Inward *et al*. (2012); [11]Koštál *et al*. (2011); [12]Langor and Raske (1987); [13]Lester and Irwin (2012); [14]Lombardero *et al*. (2000a); [15]McKee and Aukema (2015a); [16]McKee and Aukema (2015b); [17]Miller and Werner (1987); [18]Régnière *et al*. (2012); [19]Ryan (1959); [20]Safranyik *et al*. (1990); [21]Scott and Berryman (1972); [22]Wagner *et al*. (1983); [23]Wermelinger and Seifert (1998).

conditions, and by which individuals are seasonally synchronized (Tauber *et al*., 1986). Diapause has been demonstrated or suggested to occur in multiple bark beetles, although only a small proportion of species have been investigated. When diapause is induced by specific environmental conditions, it is termed facultative. Alternatively, obligatory diapause occurs regardless of environmental conditions. Facultative or obligatory diapause in the adult stage has been observed or suggested for eight bark beetle species, and a facultative larval/prepupal diapause has been found in three species (Table 10.1). Some species, including *D. rufipennis*, have both an adult and a prepupal diapause. The obligatory adult reproductive diapause provides protection from cold, and the larval/prepupal diapause aids in synchronicity and seasonality, and also reduces the probability that cold-sensitive pupae are not present during winter. The facultative nature of the prepupal diapause provides flexibility, allowing beetles to shift between semivoltinism and univoltinism depending on environmental conditions. If oviposition occurs during a cool summer, prepupal diapause is elicited and the first winter is spent as a prepupa and the second as an adult, resulting in a semivoltine life cycle. If conditions are warm during the first summer, the prepupal diapause is averted and a univoltine life cycle results. A facultative, rather than obligatory, diapause will increase the probability of decreased generation time when warming associated with climate change reduces the occurrence of dormancy in the first year.

Cold hardening

Arrested development, either via diapause or simple quiescence, does not ensure overwinter survival. Bark beetles rely on supercooling for overwintering success. The capacity to supercool has been found in all bark beetle species investigated (Table 10.1), and a physiological independence between cold hardening and diapause occurs in at least some species. As in other insects, cold hardening and diapause can, but need not, co-occur. Bark beetles are freeze-intolerant, meaning they cannot survive ice formation within their tissues (Lee, 1991). Supercooling to survive subfreezing temperatures is accomplished by accumulating antifreeze proteins and low molecular weight polyols and sugars (Table 10.1). Supercooling points (i.e. the temperature at which mortality occurs) are often much lower than the temperatures experienced, can be highly variable at a given point in time, and are higher in southern than in northern populations, most likely a genetic adaptation to local climate (Bentz and Mullins, 1999; Lombardero *et al*., 2000a). Species that inhabit colder areas exhibit seasonality in cold-hardening and cryoprotectant accumulation, with the greatest supercooling capacity in winter (Bentz and Mullins, 1999), whereas species in warm habitats show little seasonal variation in cold-hardening capacity (Lombardero *et al*., 2000a). Overwintering behaviour can also play a role in seasonality and intensity of supercooling, whereby species that typically overwinter under the bark have supercooling points lower than those of species that overwinter in the soil (Table 10.1). Overwintering in the soil can also result in a shift in the seasonality of supercooling, whereby cold-hardiness is greatest during autumn when there is a lack of snow cover (Lombardero *et al*., 2000a). A diminishing snow pack, which is predicted in a changing climate, could remove an important thermal buffer for many species that overwinter in the soil or beneath the bark of trees' lower stems. In general, increasing minimum temperatures associated with climate change can release populations from the constraint of periodic cold temperature extremes (Régnière and Bentz, 2007; Preisler *et al*., 2012; Sambaraju *et al*., 2012). It is important to note, however, that winter temperatures are not necessarily a constraint for populations across the range of all species (Trân *et al*., 2007; Weed *et al*., 2015). In addition, for some species, continued increases in minimum winter temperature could actually be detrimental if temperatures warmed to the extent that metabolic activity was accelerated and stored resources were depleted (Irwin and Lee, 2003).

Effects of temperature on community associates

Temperature also affects bark beetles indirectly through impacts on their microbial associates. In addition to the microorganisms described above, various species of nematodes and mites are commonly phoretic on bark beetles (Cardoza *et al*., 2008). Although the impact of temperature on the complex web of interactions among bark beetle microbial associates is not well known, it has been shown that certain ophiostomatoid fungi have different temperature-dependent thresholds and development rates (Hofstetter *et al*., 2007; Rice *et al*., 2008), thereby allowing the beetles to exist across a broad range of environmental conditions. Varying temperatures among and within years appears to maintain the presence of two important fungal associates of *D. ponderosae* (Addison *et al*., 2013). The influence of climate change on natural enemies that have adapted life history strategies, such as diapause, to coincide developmental timing with their prey/hosts (Reeve, 2000) will also need to be considered.

10.3.2 Effects of drought and temperature on conifer physiology, defence and detection by beetles

Rising temperatures and regional precipitation decreases will increase drought stress on many coniferous forests by increasing evaporative demand or vapour pressure deficit (Williams *et al*. 2012; Breshears *et al*., 2013). During drought, many conifers close stomata to prevent extreme negative water potentials that cause air emboli in xylem cells (i.e. cavitation) and consequently reduce sapwood hydraulic conductance (Martínez-Vilalta *et al*., 2004; Choat *et al*., 2012). Some conifers experience frequent occurrence and repair of cavitation in leaves and twigs, via mechanisms that remain poorly understood (Brodersen and McElrone, 2013). Protection of xylem from cavitation by stomatal closure reduces photosynthesis to near zero during severe drought (Plaut *et al*., 2012; Koepke and Kolb, 2013), which suggests alteration of tree carbon balance.

Drought impacts on conifer carbon balance are complex. Mild drought typically has little impact on non-structural carbohydrate (NSC) concentrations (Gruber *et al*., 2011), or can increase concentrations of specific tissues when carbohydrate use (sink strength) is reduced more than the supply from photosynthesis (source strength; Sala *et al*., 2012). This increase in tissue NSC concentration during mild drought increases the soil-to-plant water potential gradient, and consequently plant water uptake, thus serving as a drought resistance mechanism (Pallardy, 2008).

In contrast to mild drought, severe prolonged droughts often deplete NSC concentration of conifer tissues. Isohydric conifers that sharply reduce stomatal conductance to prevent cavitation, the ‘wait-it-out strategy’ (Mitchell *et al*., 2013), are prone to NSC depletion and carbon starvation (McDowell *et al*., 2008). For example, experimental severe drought reduced NSC concentration of *Pinus edulis* sapling leaves and branches by 30–50% (Adams *et al*., 2013b; Anderegg and Anderegg, 2013), *Picea abies* sapling roots by 85% (Hartmann *et al*., 2013b) and *Pinus radiata* seedlings by 48% (Mitchell *et al*., 2013). Consistent with carbon starvation, sapwood NSC concentration was almost entirely depleted during drought-induced mortality of mature *Pinus sylvestris* (Galiano *et al*., 2011). Mechanisms by which severe drought reduces conifer NSC concentration are not fully understood, but probably involve: long periods of near-zero photosynthesis during continuing tissue respiration; canopy defoliation; disruption of starch conversion to sugar; and impeded carbohydrate translocation among tissues (Breshears *et al*., 2009; Sala *et al*., 2010; Galiano *et al*., 2011; Adams *et al*., 2013b; Hartmann *et al*., 2013a). Moreover, rising temperature accelerates carbon starvation during drought because warming increases the maintenance costs of tissue respiration (Zhao *et al*., 2013).

Resin synthesis depends on NSC supply to polyphenolic parenchyma cells in xylem and phloem because carbon is the dominant elemental component of resin (Franceschi *et al*., 2005). Stored NSC is used to synthesize both constitutive (Gaylord *et al*., 2013) and induced (Guérard *et al*., 2007) resin defences. Decreases in induced resin flow during stresses that reduce photosynthesis suggest an important role of new carbon assimilation for induced defence (Lewinsohn *et al*., 1993; Lombardero *et al*., 2000b; Wallin and Raffa, 2001; Wallin *et al*., 2003). Mature conifers that have survived severe drought and associated bark beetle attacks often have more abundant or larger xylem resin ducts than trees that have died (Kane and Kolb, 2010; Gaylord *et al*., 2013). Thus, climate changes affecting NSC availability seem likely to alter conifer resin defence.

Drought has non-linear impacts on quantities of conifer resin, consistent with the growth differentiation balance hypothesis (GDBH). The GDBH predicts that moderate water stress increases resin quantity because growth is constrained more than NSC supply from photosynthesis, thereby providing surplus NSC for resin synthesis (Herms and Mattson, 1992). In contrast, GDBH predicts that severe water stress reduces the supply of NSC to all carbon sinks, including resin synthesis, due to decreased photosynthesis while NSC is depleted by tissue respiration. The GDBH has been supported for mature conifers by demonstration of a variable role of drought on the resin quantity of *Pinus taeda*, depending on the relative impact of drought on photosynthesis and within-tree carbon sink strength (Dunn and Lorio, 1993; Lorio *et al*., 1995; Reeve *et al*., 1995). Application of the GDBH to climate change suggests that increased frequency of moderate water stress will enhance resin quantity, whereas increased frequency of severe water stress, as is predicted during climate change for many water-limited forests (Vose *et al*., 2012), will reduce resin quantity. These relationships can be complex, however, because in some cases trees respond to drought with both reduced growth and increased susceptibility to bark beetles (Rolland and Lemperiere, 2004). An additional complication is that drought can result in less cambial growth, so that separate from increasing tree susceptibility, drought could reduce the food quality for developing beetles in successfully attacked trees.

Climate change also may alter resin defences indirectly via changes in tree growth. Manipulative experiments (Way and Oren, 2010) and modelling (Luo *et al*., 2008) show that warming and increased precipitation generally increase tree growth, whereas warming and reduced precipitation or water availability decrease growth. Elevated atmospheric carbon dioxide concentration increases the growth of young conifers via increased photosynthesis (Franks *et al*., 2013) and also increases resin quantity for non-suppressed trees by providing more NSC for resin synthesis (Novick *et al*., 2012). Tree growth and size are related positively to both resin flow (Davis *et al*., 2012; Westbrook *et al*., 2013) and tree survival of some bark beetle attacks (Waring, 1983; Negrón *et al*., 2009). Thus, physical resin defence may increase with climate warming via faster tree growth in cool mesic and boreal forests whose growth is currently limited most strongly by low temperature (Boisvenue and Running, 2006; Littell *et al*., 2010). In contrast, physical resin defence likely will decrease with climate warming in xeric forests where intensification of drought stress decreases tree growth (Williams *et al*., 2010). Physical resin defence may be altered further during climate change via increases in air and phloem temperatures that decrease resin viscosity and consequently increase resin volumetric flow rate from beetle attack wounds (Gaylord *et al*., 2007).

Little is known about how warming and drought affect the chemical constituents of conifer resin defences. Most investigations used seedlings rather than larger trees. In controlled manipulations, moderate drought stress yielded the highest constitutive monoterpene cyclase activity in *Abies* seedlings (Lewinsohn *et al*., 1993). In contrast, the highest induced concentrations in response to simulated attack were in well-watered seedlings (Lewinsohn *et al*., 1993). Experiments on *Pinus* and *Picea* seedlings have produced mixed results, with reports of both small (Lusebrink *et al*., 2011) and large (Turtola *et al*., 2003) changes in monoterpene quantities and composition in response to experimentally induced water stress. In one of few investigations of mature trees, experimentally induced water stress on *P. taeda* increased concentrations of resin monoterpenes, especially α- and β-pinene, but decreased concentrations of resin acids (Hodges and Lorio, 1975). This change in resin composition was suggested to increase beetle detection of stressed trees, promote beetle aggregation and reduce tree physical defence via reduction in resin viscosity and crystallization rate (Hodges and Lorio, 1975).

Warming and increasing drought intensity may influence bark beetle detection of stressed trees via a change in attraction cues. Bark beetles use a combination of visual, tactile, auditory, gustatory and olfactory cues to select trees for attack (Raffa and Berryman, 1982a; Wood, 1982; Strom *et al*., 2001). Tree monoterpenes, volatile organic compounds and ethanol are olfactory attractants for some bark beetles (Kelsey and Joseph, 2001; Seybold *et al*., 2006; Miller and Rabaglia, 2009). Drought stress could alter tree quantity and/or composition of these attractants (e.g. Manter and Kelsey, 2008), which in turn could signal tree stress to bark beetles.

Cavitation of water in sapwood is another potential signal of conifer stress that may be altered by climate change-induced drought. Sapwood cavitation causes ultrasonic acoustic emissions that are detectable with transducers at the bark surface (Rosner *et al*., 2006). Some bark beetles respond to ultrasonic acoustic waves at frequencies similar to those produced by sapwood cavitation during drought (Rudinsky and Michael, 1972). The hypothesis that acoustic emissions from sapwood cavitation signal tree stress to bark beetles has not been tested adequately.

10.3.3 Effects of temperature and drought and their interactions on recent outbreaks

There is substantial empirical evidence for climate influences on recent bark beetle outbreaks in North America, particularly *D. ponderosae*, *D. rufipennis*, *D. frontalis*, and *Ips confusus* LeConte. Studies in the USA and Canada have relied on aerial surveys from forestry agencies, archived records of outbreaks (e.g. Hebertson and Jenkins, 2008) and dendrochronological analyses (e.g. Berg *et al*., 2006; Campbell *et al*., 2007). Ideally, studies include variables that represent each of the major influences of climate discussed previously. In practice, a range of climate variables has been used, from simple climate variables to outputs of climate suitability models (e.g. Preisler *et al*., 2012).

The influence of climate on bark beetle outbreaks has been documented in several respects. First, observed range expansion of outbreaks has been linked to climate (Section 10.4.1). Second, temperature increases that provide more favourable conditions for the beetles, and drought stress that provides more susceptible hosts, have facilitated outbreaks within historical ranges (Berg *et al*., 2006; Rouault *et al*., 2006; Aukema *et al*., 2008; Raffa *et al*., 2008). Warmer winters and higher year-round temperatures benefit beetles directly and have been identified as facilitating outbreaks (Aukema *et al*., 2008; Powell and Bentz, 2009; Marini *et al*., 2012; Preisler *et al*., 2012; Creeden *et al*., 2014). Drought conditions exert stress on host trees, reducing their defences and thus facilitating outbreaks (Raffa *et al*., 2008; Creeden *et al*., 2014; Hart *et al*., 2014). In some cases, the effect of drought can be spatially explicit, such as when drier sites provide the basis for initial population increases that can subsequently transition into regional outbreaks (Kaiser *et al*., 2014). The seasonal timing of water stress can also be important (Thomson and Shrimpton, 1984; Hebertson and Jenkins, 2003; Raffa *et al*., 2008; Preisler *et al*., 2012). Populations of non-aggressive beetle species are closely tied to drought effects on host susceptibility during both their rising and falling phases (Raffa *et al*., 2008). In contrast, relief from drought does not terminate outbreaks of aggressive species when populations have exceeded a critical threshold (Raffa *et al*., 2008; Creeden *et al*., 2014). Third, unfavourable temperatures can lead to declines in outbreaking populations of aggressive bark beetles. For example, low winter temperatures appear to have reduced *D. ponderosae* populations in British Columbia in the 1980s (Safranyik and Linton, 1991; Stahl *et al*., 2006) and early 1930s (Bentz *et al*., 2011). Unusually low summer temperatures (without low winter temperatures) reduced building populations of *D. ponderosae* in Idaho in 1993 (Logan and Powell, 2009; Creeden *et al*., 2014). Declines of several *D. ponderosae* outbreaks did not occur under unfavourable climate conditions, however, suggesting roles of other factors, such as host depletion (Creeden *et al*., 2014).

There are several key areas in which our knowledge remains relatively limited. In particular, studies of actual beetle population responses, rather than just killed trees, to climate change would increase the confidence of findings. The lack of such observations over larger spatial extents and/or longer periods, and also at the critical fine scales at which populations first rise, makes it difficult to delineate thresholds. Likewise, we have little understanding of how climate change will influence disturbance interactions. For example, anticipated changes in temperature and precipitation regimes are projected to increase the frequency and severity of wildfires (Westerling *et al*., 2011). By itself, wildfire injury is unlikely to elicit large-scale outbreaks (Hood and Bentz, 2007; Davis *et al*., 2012; Powell *et al*., 2012). However, as climatic drivers increasingly raise beetle populations and exert region-wide stress on host trees, the likelihood that immediate population increases following fire could transition into outbreaks through their combined and interacting effects may increase.

10.4 Effects of Climate Change on Bark Beetle Range Expansion and Population Dynamics in New Habitats

When evaluating how relationships between plants and herbivores may respond to climatically induced herbivore range shifts, it is useful to delineate three general types of regime change: (i) increased and more persistent establishment in areas where host trees historically experienced only intermittent exposure (semi-naïve); (ii) establishment in areas dominated by a historical host tree species but where local tree populations had experienced little or no pressure (naïve host); and (iii) movement into new areas that contain tree species that had not experienced prior exposure and are connected via suitable host type to historically unexposed biomes (naïve novel host). It is most useful to base degrees of historical interaction and reproductive range on evidence of actual beetle development in hosts, as opposed to just sedimentation layers, because advective transport can randomly deposit large numbers of insects (Jackson *et al*., 2008; de la Giroday *et al*., 2011) and thus generate false positives.

10.4.1 Recent changes in latitudinal, elevational and host species ranges of bark beetles

To avoid local extinction during rapidly changing climate, organisms must migrate to more favourable habitats, respond with phenotypic plasticity in thermally dependent traits and/or adapt genetically to changing conditions (Hoffmann and Sgrò, 2011). The distribution of many tree-killing bark beetles is currently limited by climate, rather than host trees (Bentz *et al*., 2010; Weed *et al*., 2013), allowing opportunities for expansion of outbreak populations with warming, particularly to the north (Carroll *et al*., 2004; Trân *et al*., 2007; Cullingham *et al*., 2011; de la Giroday *et al*., 2012). Although few studies have been conducted on bark beetles, phenotypic plasticity is evident when beetles are reared in different environments, such as thick versus thin phloem (Haack *et al*., 1987), across environments and different temperatures (Bentz *et al*., 2011; Bracewell *et al*., 2013) and among years with different thermal patterns (Bentz *et al*., 2014). Continued warming, however, could exceed the range of plastic tolerance for some species and occur faster than potential adaptation, even within insects that have relatively short generation times. Given sufficient time, genetic variation and strong selection, populations could further adapt to novel thermal regimes and affect outbreak risk (Björkman *et al*., 2011). The potential for necessary changes in bark beetle species at the genetic level, however, is poorly understood.

Two common responses of ectotherms to elevated temperature are movement into higher elevations and movement into higher latitudes (Parmesan, 2006). Bark beetles are no exception, and there are well-documented examples involving several species (Table 10.2). Increases in both winter and year-round temperatures have contributed to northward (Carroll *et al*., 2004; Trân *et al*., 2007; Safranyik *et al*., 2010; Sambaraju *et al*., 2012) and elevational (Logan and Powell, 2001; Logan *et al*., 2010) movement of *D. ponderosae*, including into forest types that have experienced no or infrequent beetle activity in the past. Similarly, increasing winter minimum temperatures in New Jersey have allowed the persistence of outbreak-level populations of *D. frontalis* (Weed *et al*., 2013).

10.4.2 Anticipating trophic interactions with host trees and natural enemies in semi-naïve and naïve habitats

In addition to the direct effects of temperature, a wide range of trophic interactions will influence the extent to which insect populations establish, spread and undergo outbreaks in newly or increasingly accessed habitats. These drivers include multiple components of plant–insect relationships, interactions with natural enemies such as predators, parasitoids and competitors, and mediation of these relationships by beetles' symbionts. Our ability to predict how these relationships will affect beetle performance in changing climate scenarios is poor, but our understanding of outbreak dynamics in historical ranges (Fig. 10.1) can provide a useful framework.

Table 10.2. Range expansions of bark beetles, and population dynamics in new habitats, associated with climate change.

Species	Region	Shift in latitude, elevation and/or host species	References
Dendroctonus ponderosae	Western North America	Upward shift in elevation, permitting increased access to high-elevation five-needle pines	Logan and Powell (2001); Carroll *et al*. (2004); Hicke *et al*. (2006); Bentz *et al*. (2010); Logan *et al*. (2010); Raffa *et al*. (2013)
D. ponderosae	Western Canada	North and eastward shifts, permitting access to jack pine	Cerezke (1995); Jackson *et al*. (2008); Robertson *et al*. (2009); Cudmore *et al*. (2010); Safranyik *et al*. (2010); Cullingham *et al*. (2011); de la Giroday *et al*. (2011, 2012); Sambaraju *et al*. (2012)
Dendroctonus brevicomis	Western USA	Modelled future range expansion and contraction predictions	Evangelista *et al*. (2011)
Dendroctonus frontalis	Southern USA	Northward range expansion	Ungerer *et al*. (1999); Waring *et al*. (2009)
D. frontalis	Eastern USA	Northern expansion of outbreaks in New Jersey pinelands	Weed *et al*. (2013)
Dendroctonus mexicanus	South-western USA	Northward range expansion	Moser *et al*. (2005); Waring *et al*. (2009)
Ips pini	Western USA	Modelled future range expected to decrease generally	Evangelista *et al*. (2011)

Range responses to climate change have been most studied in *D. ponderosae*, so we focus on this system as a case study. Forest types in the northern Rocky Mountains show strong elevational gradients (Logan and Powell, 2001). Middle elevation stands are typically dominated by lodgepole pine, which transition into non-host species such as spruce and fir, and higher elevations are dominated by five-needled pine species such as whitebark pine. Over the periods for which data are available, most mortality caused by *D. ponderosae* was to lodgepole pine, with only intermittent and comparatively brief impacts on whitebark pine during unusually warm periods (Logan and Powell, 2001; Jewett *et al*., 2011). As unfavourable conditions such as cold temperatures returned, beetle populations either declined below detectable levels or became locally extirpated (Logan *et al*., 2010). During recent years, however, continuous high temperatures have been accompanied by continuous *D. ponderosae* reproduction and high tree mortality in stands dominated by five-needled pines (Logan *et al*., 2010).

In mixed stands that provided equivalent environmental conditions, lodgepole pines had higher total concentrations of constitutive phloem monoterpenes than whitebark pines (Raffa *et al*., 2013). Differences in inducible defences were even more striking. When trees were challenged with simulated attack by *D. ponderosae*–*Grosmannia clavigera* complexes, lodgepole pine showed much greater induced biosynthesis of monoterpenes. Resin flow in response to natural attacks was also more substantial in lodgepole pines. There were also differences in the composition of phloem chemicals that related to beetle performance. Whitebark pines had higher concentrations of the pheromone precursor (Blomquist *et al*., 2010) (–)-α pinene and the pheromone synergist (Miller and Borden, 2000) myrcene, and lower concentrations of the repellent (Sturgeon and Mitton, 1986) limonene and lower induced concentrations of the pheromone inhibitor 4-allylanisole (Emerick *et al*., 2008) than whitebark pine. Collectively, these results suggest that whitebark pine is relatively poorly equipped to prevent mass attacks from being elicited by pioneer beetles, and to resist attacks under way. Overall, both the tree defence and temperature sides of the portal in Fig. 10.1 appear to widen with anticipated climate change, making continued outbreaks in high-elevation ecosystems more likely.

Host selection behaviour adds an additional, and complicating, dimension to beetle–host relationships. In the above mixed stands, beetles entered more lodgepole than whitebark pines, despite the latter's inferior defences. Thus, there appears to be a lag time between increased access to a less defended tree and increased behavioural orientation toward it. Although beetles may not prefer whitebark pines, they readily accept them. For example, in no-choice laboratory assays, beetles entered both trees equally, and in stands dominated by whitebark pine, natural entry rates were equivalent. These results resemble findings from other systems that delineate the timespans and complexity of host switching by herbivorous insects (Singer and McBride, 2010). Presumably, there will be increased selection for orientation toward whitebark pine if warm temperature regimes persist.

We currently have little information on how a third constraint in Fig. 10.1, predators, competitors and symbionts, compares between lodgepole and whitebark pine habitats. The little data available suggest that predators and competitors may, like the herbivore, display lags in their host-searching behaviours. These insects find beetle-killed trees by exploiting volatile plumes containing mixtures of bark beetle pheromones and tree compounds (Wood, 1982). In the mixed stands described above, numbers of the major predator and competitor species were equivalent in unbaited traps on unattacked lodgepole and whitebark pines (Raffa *et al*., 2013). However, more of these predators and competitors were caught on lodgepole than on whitebark pines in which *D. ponderosae* were tunnelling. Additional behavioural studies are needed to determine how prevalent and persistent this pattern is, and whether *D. ponderosae* attacking whitebark pines may experience partial escape from natural enemies. In addition, the relative abundances of predators and competitors in lodgepole versus whitebark pine stands are unknown.

The second type of regime change, establishment in areas predominantly covered by the same, but historically unexposed, host species (naïve habitats), has also been observed with *D. ponderosae* (Safranyik and Carroll, 2006; Safranyik *et al.*, 2010). Large-scale outbreaks in the predominantly lodgepole pine forests of southern British Columbia have been well documented over the past several hundred years. The beetle's historical distribution was limited by cold temperatures to the north and the geophysical barrier of the Rocky Mountains to the east (Carroll *et al.*, 2004; Sambaraju *et al.*, 2012). More recently, beetles have moved farther north, where they have caused extensive mortality to lodgepole pines (Carroll *et al.*, 2004; Sambaraju *et al.*, 2012). Additionally, these high populations provided the source for windborne eastward dispersal in enormous and proably unprecedented numbers (Bartell *et al.*, 2008; Jackson *et al.*, 2008). Beetles recently breached the Rocky Mountains in west-central Alberta and are now causing high mortality in the lodgepole pine forests of western Alberta (de la Giroday *et al.*, 2012).

As with increased beetle access to high-elevation stands, we have little knowledge of trophic interactions in regions recently accessed by *D. ponderosae*. However, the available data indicate beetle reproduction is higher in historically unexposed than exposed lodgepole pine habitats (Cudmore *et al.*, 2010). Naïve lodgepole pine appears to be both more susceptible and of higher quality for beetle development (Fig. 10.2). This is consistent with limited prior selection pressure imposed by *D. ponderosae* on these trees. Furthermore, lodgepole pines in areas that did not historically experience beetle outbreaks had higher levels of the pheromone precursor α-pinene (Clark *et al.*, 2010) and lower overall concentrations of induced monoterpenes (Clark *et al.*, 2010, 2014). This suggests host trees in naïve habitats are both more likely to facilitate mass attacks and less able to defend themselves. Thus, it appears that both the left and lower margins of the eruptive window in Fig. 10.1 will be more favourable to *D. ponderosae* in naïve lodgepole pine habitats under anticipated climate regimes.

Information comparing natural enemy and competitor complexes between lodgepole pines in historically versus recently infested regions is not available. Likewise, our knowledge of the microbial associates in historically exposed versus unexposed regions is limited. Both the relative abundance of the ophiostomatoid fungi (Rice *et al.*, 2008) and the complex of bacteria (Adams *et al.*, 2013) associated with *D. ponderosae*–lodgepole pine complexes

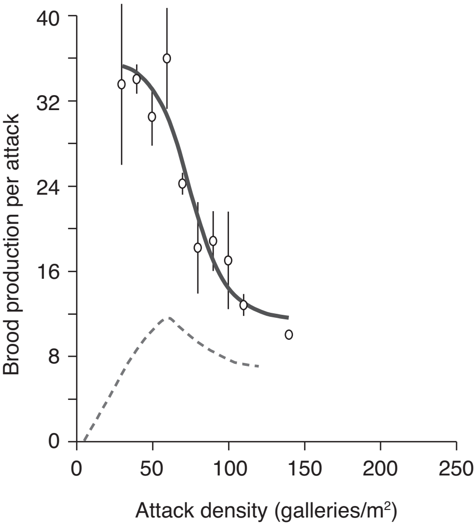

Fig. 10.2. Mean (±SE) number of mountain pine beetle offspring per female in relation to the density of attacking females determined from 10 to 12 mass attacked lodgepole pines within each of 8 infestations assessed in 2008 near Grande Prairie, Alberta, Canada (A.L. Carroll, unpublished data). The same relationship for mountain pine beetle attacking lodgepole pine within its native range (north-eastern Oregon, USA (from Raffa and Berryman, 1983)) is shown as a dashed line. Lodgepole pines in the naïve zone are both more susceptible, evidenced by the peak of the solid line occuring much farther to the left than the peak of the dashed line, and are also of higher substrate quality (phloem thickness, nutrients, symbiont activity, etc.), evidenced by any point past the peak of the dashed line being higher than that of the solid line.

appear to differ between British Columbia and Alberta, but the biological significance is unknown.

With increased temperatures, *D. ponderosae* is also undergoing the third type of regime change, spread into entirely new (naïve, novel host) habitats (Logan and Powell, 2001; Safranyik *et al.*, 2010). Lodgepole pine naturally hybridizes with jack pine in sections of Alberta, and both hybrid and pure jack pines are being killed (Cullingham *et al.*, 2011). Jack pine extends eastward through the boreal forest and connects with eastern white pine and red pine in the Great Lakes region. This raises the prospect of a 'native invasive' whereby anthropogenically altered climate rather than direct human transport provides the bridge (Erbilgin *et al.*, 2013; Lusebrink *et al.*, 2013). Models of temperature suitability for beetles yield variable predictions (Bentz *et al.*, 2010; Safranyik *et al.*, 2010).

In estimating how trophic interactions will influence *D. ponderosae* in habitats dominated by naïve host species, we consider in sequence host-plant relationships, forest structure and natural enemies and symbionts (Fig. 10.1). Table 10.3 provides data on the same host compounds evaluated in the lodgepole versus whitebark pine comparison. Several trends emerge. First, the naïve novel tree species, especially in the Great Lakes region, appear more amenable to *D. ponderosae*'s mass attack behaviour than the historical species (Erbilgin *et al.*, 2013; Raffa, 2014; Clark *et al.*, 2014). For example, jack pine has a higher per cent composition of α-pinene than lodgepole pine. Further, none of the pheromone inhibitor, 4-allylanisole, was found in jack pine. Concentrations of myrcene, a pheromone synergist, appear within the range of lodgepole pine. Red pine has higher concentrations of α-pinene than lodgepole pine and no detectable levels of 4-allylanisole. Eastern white pine had higher levels of α-pinene and lower levels of 4-allylanisole than lodgepole pine. A second trend is that there is substantial intraspecific variation between regions. Interestingly, Alberta lodgepole pine had higher concentrations of α-pinene, that is, were more jack pine-like, than the British Columbia, Oregon or Wyoming populations, and Alberta jack pine had lower concentrations, that is, were more lodgepole pine-like, than the jack pines in Wisconsin. This is consistent with the hybridization by these species in Alberta. With regard to inducibility, midwestern pines show pronounced biosynthesis of monoterpenes and

Table 10.3. Composition (%) of volatiles known to affect bark beetle signalling in lodgepole versus midwestern pines.

	Host volatile			
Pine species (region)	α-pinene	Myrcene	4-Allylanisole	Reference
Lodgepole (central southern British Columbia)	5.26	0.73	Not tested	Boone *et al.* (2011)
Lodgepole (eastern central British Columbia and western central Alberta)	7.09	2.98	Not tested	Clark *et al.* (2014)
Lodgepole (north-western Wyoming)	3.27	3.96	1.05	Powell and Raffa (2011)
Lodgepole (north-eastern Oregon)	2.92	1.66	Not tested	Raffa and Berryman (1982b)
Lodgepole (western central Alberta)	23.26	2.00	Not tested	Erbilgin *et al.* (2013)
Jack (eastern central Alberta)	58.42	2.16	Not tested	Clark *et al.* (2014)
Jack (eastern northern Alberta)	58.12	1.09	Not tested	Erbilgin *et al.* (2013)
Jack (central Wisconsin)	71.04	3.83	0.00	Aukema *et al.* (2010)
Red (central Wisconsin)	60.66	0.41	0.00	Aukema *et al.* (2010)
Eastern white (central Wisconsin)	64.45	1.98	0.42	Aukema *et al.* (2010)

phenolics in response to fungi vectored by the bark beetles native to this region (Raffa and Smalley, 1995). However, Clark *et al.* (2014) found that induced monoterpene biosynthesis to mountain pine beetle-associated fungi was lower in jack pine than in southern British Columbia lodgepole pine. So, while naïve novel host species have evolved defences to local ophiostomatoid fungi, it is unclear whether those defences are effective against *D. ponderosae* and its associated microorganisms. An additional feature that could potentially increase tree susceptibility in the boreal forest and Great Lakes region is biotic stress caused by a native outbreak defoliator, *Choristoneura pinus pinus* Freeman, which reduces defences in jack pine (Wallin and Raffa, 2001; Colgan and Erbilgin, 2011) and root beetles (*Hylobius*, *Hylastes*) and associated fungi that impair defences in red pine (Klepzig *et al.*, 1996; Aukema *et al.*, 2010).

It is not known whether the structure of midwestern boreal forests will be as conducive to outbreaks as that of Rocky Mountain lodgepole pine forests (Fig. 10.1, upper margin). Lodgepole forests tend to be dense, of low species diversity and of relatively even age structure (Taylor and Carroll, 2004). Boreal forests tend to be much more fragmented, with jack pines often distributed patchily amid aspen, prairie and other habitats (Safranyik *et al.*, 2010). These structural features decrease the likelihood of synchronous, landscape-scale outbreaks. Additionally, if jack pines in the region have relatively thinner phloem or smaller diameters, that could limit brood production in killed trees. Although much more research is needed, preliminary considerations suggest this element of the eruptive window might be narrowed.

Another factor that could potentially help narrow the eruptive window of *D. ponderosae* in midwestern forests is the abundance of predators and competitors. Overall, predator and competitor loads of midwestern beetles appear to be higher than those of western beetles (Table 10.4). The transcontinentally distributed *D. rufipennis* provides a case study for appraising inter-regional effects. In this system, predator and competitor loads are much higher in the Midwest. Table 10.4 probably underestimates the increased competitor load that invading *D. ponderosae* would encounter, because the primary tree-killing bark beetle of midwestern pines, *Ips pini*, is a secondary beetle, i.e. competitor, where it overlaps *D. ponderosae*. Also, a survey of *Monochamus* (Cerambycidae) species (Miller *et al.*, 2013), which can be significant competitors and facultative predators of tree-killing bark beetles (Dodds *et al.*, 2001), reported a mean trap catch 1.5 times higher in Wisconsin and Michigan than in seven western states and provinces. The extent to which these communities would influence *D. ponderosae* in new habitats, however, is unknown. An important question concerns how strongly natural enemies in midwestern forests are attracted to *D. ponderosae*'s pheromones. If they are abundant but not attracted to the newly arrived pest, their effect could be diminished. We currently lack data on these predators' responses to the transverbenol produced by female *D. ponderosae*, but at least three local bark beetles (*D. rufipennis*, *D. simplex* and *Dendroctonus valens*) produce frontalin, which male *D. ponderosae* emit. The major predators in upper midwestern forests are highly attracted to this compound (Aukema and Raffa, 2005). Another factor that could improve attraction to *D. ponderosae* is that secondary arrival by *I. pini* results in the emission of ipsdienol, which attracts predators that subsequently feed on *D. ponderosae* (Boone *et al.*, 2008). A second question concerns the phenological synchrony between *D. ponderosae* and natural enemies in midwestern forests. For example, *D. ponderosae* typically attacks trees in mid to late summer, whereas most predators in Wisconsin are active earlier in the season (Aukema *et al.*, 2000). This asynchrony could potentially provide *D. ponderosae* with some escape from the high populations of predators there.

10.5 Conclusions

1. Both mechanistic understanding of the key processes affecting bark beetle population dynamics, and epidemiological

Table 10.4. Predator and competitor loads of bark beetles in western versus midwestern North America. Studies that were designed deliberately to manipulate ratios of predators and prey were omitted; direct comparisons or meta-analyses were not applicable due to interspecific and methodological differences. Table 10.4a = arrival; Table 10.4b = emergence.

(a)

Location	Primary bark beetle	Predators/ beetle	Competitors/ beetle	Reference	Sampling method
Western region					
Interior Alaska	*Dendroctonus rufipennis*	Not sampled	2.00	Werner *et al*. (2006)	Pheromone traps
British Columbia	*Dendroctonus ponderosae*	0.01	Not sampled	Miller *et al*. (2005)	Pheromone traps
North-eastern Oregon	*Dendroctonus pseudotsugae*	0.04	Not sampled	Ross and Daterman (1995)	Pheromone traps
North-eastern Oregon	*D. pseudotsugae*	0.14	Not sampled	Ross and Daterman (1997)	Pheromone traps
North-eastern Oregon	*D. pseudotsuga, D. brevicomis*	0.02	0.07	Zhou *et al*. (2001)	Pheromone traps
West-central Montana	*D. ponderosae*	0.67	1.25	Boone *et al*. (2008)	Pheromone traps
North-western Wyoming	*D. ponderosae*	0.06	2.54	Raffa *et al*. (2013)	Unbaited funnel traps
North-western Wyoming	*D. ponderosae*	0.00	0.01	Powell *et al*. (2012)	Pheromone traps
North-eastern Utah	*D. ponderosae*	Not sampled	2.37	Lerch (2013)	Unbaited panel traps
Great Lakes region					
North-eastern Minnesota	Mostly *Dendroctonus simplex*, some *D. rufipennis*	0.99	3.25	Gandhi *et al*. (2009)	Pheromone traps
Northern Minnesota, Wisconsin, Michigan	*Dendroctonus rufipennis*	204.50	402.25	Haberkern and Raffa (2003)	Pheromone traps
Wisconsin	*Ips pini*	2.12	0.09	Aukema and Raffa (2004)	Attraction to infested bolts
Wisconsin	*I. pini*, *Ips grandicollis*	0.10	Not sampled	Erbilgin *et al*. (2002)	Pheromone traps
Wisconsin	*I. pini*	1.59	Not sampled	Erbilgin and Raffa (2000)	Infested bark disks
Wisconsin	*I. pini*	0.71	0.06	Raffa (1991)	Pheromone traps

continued

analyses relating tree mortality to environmental factors, provide strong evidence that outbreaks are largely driven by weather. These include both direct and host-mediated effects. Specifically, warm temperatures can reduce overwintering mortality and shorten generation times, and severe drought and warm temperatures impose physiological stresses on trees that can impede their defence systems.

Table 10.4. *continued.*

(b)

Location	Primary bark beetle	Predators/ beetle	Competitors/ beetle	Reference	Sampling method
Western region					
Interior Alaska	*D. rufipennis*	0.35	4.02	Gara *et al.* (1995)	Emergence from infested logs
Coastal Alaska	*D. rufipennis*	0.06	2.02	Gara *et al.* (1995)	Emergence from infested logs
Great Lakes region					
Northern Minnesota, Wisconsin, Michigan	*Dendroctonus rufipennis*	1.9	2003.00	Haberkern *et al.* (2002)	Emergence from infested logs

2. Several species of eruptive bark beetles exhibit bimodal population dynamics, such that if their numbers surpass a critical threshold, their growth becomes self-sustaining, even after initial inciting conditions are relaxed. Because most climate change models predict not only changes in mean temperature and precipitation but also more frequent extreme events, species that exhibit such threshold behaviour are particularly likely to undergo regime changes, with increased environmental and socio-economic impacts.

3. There is substantial evidence that recent anthropogenic changes in climate have increased the frequency and magnitude of outbreaks by some bark beetle species. Due to temperature-dependent physiological constraints, however, response to continued climatic changes will vary among and within species.

4. In addition to increased impacts within historical regions, some tree-killing bark beetles are surviving better at higher latitudes and elevations than in the past, accessing new regions in which host species historically had little exposure and accessing new regions with historically unexposed host species. In the latter cases, native bark beetles pose the risk of behaving as invasive species, linked to new biomes by climate change rather than human transport.

5. We currently lack the information needed to predict how bark beetles will behave in naïve habitats. Current population models yield different results, in part because we are just beginning to quantify phenotypic plasticity and genetic variation within species. In general, tree resistance is lower in regions that had little or no prior exposure than in historical ranges. We have only marginal information on beetle behavioural preferences. It also appears that midwestern forests may harbour richer competitor and predator communities than western conifer forests, but direct comparisons have not been performed.

6. Although there is substantial knowledge on the genetics, physiology, behaviour and ecology of bark beetles, our ability to project this information on to future temperature and precipitation regimes in historical habitats, the spread, survival and population dynamics of beetles in newly accessed regions, and the socio-economic impacts of these alterations, is limited. Indeed, one of the major consequences of climate change is increased uncertainty.

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11

The Eurasian Spruce Bark Beetle: The Role of Climate

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Abstract

The Eurasian spruce bark beetle is one of the major forest pests in Europe, capable of mass attacking and killing Norway spruce over extensive areas during outbreaks. Here, we review various aspects of its biology in relation to climatic variables. The aim of this review was to make predictions about the potential consequences of climate change on the propensity for outbreaks across European forests. More frequent extreme winds and drier and warmer summer climate may trigger both population growth and the susceptibility of spruce stands to attack. Breeding material provided by large windfall events increase the beetle population rapidly to a level capable of killing living trees through mass attack. Such epidemics may proceed until the susceptible spruces are exhausted, or when other extrinsic conditions stop the bark beetles from further colonization. At the southern margin of the spruce distribution in Europe, lower than average precipitation seems generally to favour infestations. In central and Western Europe, even-aged plantations outside the natural range of Norway spruce are highly susceptible to disturbance events such as windthrow and bark beetle attacks. A warmer climate is expected to give a northern expansion of the area experiencing two generations per year in Europe. There have been few bark beetle outbreaks in the extensive areas of spruce forest in Finland and the northern part of Scandinavia, but increasing bark beetle populations and infestations have been observed during warm years in the last decade. The northern part of Europe may be subject to huge outbreaks if a warmer climate increases the population sizes of the Eurasian spruce bark beetle.

11.1 Introduction

Large numbers of bark beetle species are associated with coniferous forest ecosystems, although relatively few of them can impact ecosystem structure and function (Raffa *et al*., 2008; Økland *et al*., 2011). More than 7500 bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae) have been described worldwide, including nearly 900 scolytid species in the Palaearctic region only (Knizek and Beaver, 2004). Among the European scolytids, only few species attack and reproduce in living trees and are considered as significant forest pests (Grégoire and Evans, 2004).

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The Eurasian spruce bark beetle (*Ips typographus* L.) is by far the most destructive species among the scolytids in the conifer forests of Europe. This 5-mm long beetle (Fig. 11.1 – picture of *I. typographus*) is one of the major forest pests in Europe, capable of mass attacking and killing mature spruce trees (Wermelinger, 2004). Its main host is Norway spruce (*Picea abies* (L.) H. Karsten), which today is the most abundant coniferous tree species in northern Europe and in many of the mountain ranges elsewhere in Europe (Global Forest Resources Assessment, 2010; The Gymnosperm Database, 2013). The Eurasian spruce bark beetle may kill host trees over extensive areas during periods of outbreak (Kausrud *et al*., 2012). For example, in ten European countries, the Eurasian spruce bark beetle killed more than 30 million m^3 of spruce during the 1990s (Grégoire and Evans, 2004). In Scandinavia, a large outbreak in the 1970s killed forests equivalent to 9 million m^3 of lumber, which at the time was worth about €114 million (Økland *et al*., 2012). In Slovakia, an ongoing outbreak has killed more than 13 million m^3 since 2005 (Nikolov, 2012).

Global warming already has, and is expected to have, further impact on the temporal and spatial dynamics of several insect herbivores (Parmesan, 2006; Jepsen *et al*., 2008; Netherer and Schopf, 2010). The Eurasian spruce bark beetle is not expected to be any exception in this respect; however, long-term empirical studies evaluating the relative importance of the direct versus the indirect effects of climate are still scarce (Marini *et al*., 2012). Thus, in the present chapter, we utilize the literature about how various aspects of the biology and distribution of the Eurasian spruce bark beetle and Norway spruce forests are related to climatic variables, to interpolate what we can expect about distributions and damages under a future climate. The literature comprises experiments, field studies and modelling approaches that contribute towards understanding the direct effects of climatic variables on life cycle, population dynamics and other relevant issues for the outbreaks of the Eurasian spruce bark beetle (Christiansen and Bakke, 1988; Wermelinger, 2004; Jönsson *et al*., 2011; Kausrud *et al*., 2012). In addition, climatic variables determine the vigour and distribution of coniferous forests in the future. Indirect effects are closely tied to the interactive dynamics between beetles and host trees during shifts in distribution of coniferous forests, and they depend on the future manifestations of climate variables in various regions of Europe.

Fig. 11.1. Eurasian spruce bark beetle, *Ips typographus*. (Photo: Karsten Sund.)

11.2 The Eurasian Spruce Bark Beetle

The development of the Eurasian spruce bark beetle is synchronized phenologically by completing either one, two or three generations per year. It usually hibernates in the adult stage, and complete development is required for survival during hibernation (Austarå *et al*., 1977; Faccoli, 2002). One generation per year is predominant in the north and at high elevations in the south of Europe, while the number of generations per year may be two or three towards the south and lower elevations in Europe (Lange *et al*., 2006; Dolezal and Sehnal, 2007; Netherer and Schopf, 2010; Wermelinger *et al*., 2012). Studies from the boreal parts of Scandinavia and Finland showed that the majority of the adults hibernated in the litter near their brood trees (Annila, 1969; Austarå *et al*., 1993). However, during warm years in southern Scandinavia (Persson *et al*., 2009) and further south in Europe, a significant proportion of the beetles hibernated under the bark of their brood trees. In Switzerland, about half of the bark beetles in univoltine populations left their brood trees, while the overwhelming majority of the second generation of populations hibernated under the bark (Wermelinger *et al.*, 2012). A study in the south-eastern Alps demonstrated a winter mortality of about 50% for Eurasian spruce bark beetle hibernating under bark, mainly for larvae and young adults (Faccoli, 2002). The beetles emerge in the spring when a required thermal sum is reached, and mass flight and search for suitable breeding material start when the daily maximum temperatures are above a sufficient level, which may vary locally in the range 16.5–20°C (Annila, 1969; Lobinger, 1994; Baier *et al.*, 2007).

At low population densities, the Eurasian spruce bark beetle breeds in fresh wind-felled or dying spruces. Natural defence mechanisms of healthy spruce trees usually repel or kill any assailants (Franceschi *et al.*, 2005). The beetles bore through the outer bark, excavate a nuptial chamber in the phloem and produce aggregation pheromones that attract conspecifics of both sexes (Christiansen and Bakke, 1988). While attracted males may initiate new chambers in the same site, one to four females may enter the chamber of the attractor. After mating, the females excavate egg tunnels and deposit eggs along the tunnel walls. The developing larvae feed on phloem and/or fungi in the larval tunnels. Intraspecific competition at high breeding densities may affect behaviour and may result in shorter maternal galleries and reduced productivity (Anderbrant *et al.*, 1985; Anderbrant, 1990).

When the local bark beetle population is larger than the access of suitable habitat in recent dead spruces, the beetles may be forced to attack living spruce trees. Successful attack leading to colonization and tree killing may require high beetle numbers to overwhelm the defence of the tree (Weslien and Lindelöw, 1989). The likelihood of a tree to be colonized by the Eurasian spruce bark beetle differs significantly among trees (Jakuš *et al.*, 2011; Schiebe *et al.*, 2012). The defence capacity and relative resistance of spruce trees depend on genetics, physiological status and chemical composition of terpenes and phenoles of the individual trees (Franceschi *et al.*, 2005; Schiebe *et al.*, 2012). Even non-host volatiles may be involved when the pioneer beetles search for suitable hosts (Zhang and Schlyter, 2004). It is largely unknown how the bark beetles pioneering an attack on a living spruce locate and choose a suitable host, but it is well known that the secondary attraction to aggregation pheromones plays a central role in the colonization of living trees (Schiebe *et al.*, 2012). Tree mortality during outbreaks of the Eurasian spruce bark beetle tends to form patchy patterns in the conifer landscapes of spruce forests (Worrell, 1983). The spread of infestations are usually strongly distance dependent, following an inverse power law function, where most of the new patches of killed spruce occur within 500 m from the previous year's infestations (Kautz *et al.*, 2011). The division of the resource base of this bark beetle species into two groups with different characteristics (newly dead and living spruce) results in complex spatio-temporal population dynamics with several direct and indirect relationships to climatic variables (Kausrud *et al.*, 2011, 2012).

11.3 Direct Effects of Climate Change

Although the Eurasian spruce bark beetle spends long periods of its life cycle under protection of the bark, climate and weather significantly determine the species' phenology and propagation. The direct influence of environmental cues on swarming and dispersal, attraction to host trees, development rates, diapause, hibernation and survival has been studied intensively in order to determine outbreak risks better (Wermelinger, 2004). A variety of models have recently been developed allowing the life cycle of spruce bark beetles to be simulated under current and future climate based on the thermal requirements of different life cycle phases (Seidl *et al.*, 2011a; Jönsson *et al.*, 2012). Commonly, these models assume total mortality of immature stages during winter (Harding and Ravn, 1985; Faccoli, 2002) and reproductive diapause (Jenkins *et al*., 2001).

Termination of reproductive diapause in the Eurasian spruce bark beetle requires a chilling period, and is followed by a state of quiescence, which in central Europe is usually achieved in December or January (Dolezal and Sehnal, 2007). Beetles do not emerge before certain thresholds of day length and thermal sums are surpassed (Annila, 1977; Zumr, 1982; Baier *et al*., 2007), and before air temperatures between 16°C and 18°C are reached (Bakke *et al*., 1977; Lobinger, 1994). Mass flight mainly takes place around noon and in the early afternoon, when air temperatures reach optimal values above 20°C (Annila, 1969; Wermelinger, 2004). Swarming is thus strongly dependent on site conditions (Austarå *et al*., 1993) and may begin as early as in April in central and southern Europe (Wegensteiner and Führer, 1991) or as late as in June in northern Europe (Annila, 1977). Unfavourable weather conditions such as strong winds or precipitation events prevent beetles from flying and attacking trees (Merker, 1952).

Pioneer beetles preferentially head for sun-exposed trees offering increased bark temperatures (Vite, 1952). These trees are often found at forest edges, margins of clear-cuts, small clearings or along forest roads (Grodzki *et al*., 2003). Hence, egg deposition and offspring development are particularly dependent on the microclimatic conditions of the inner bark. Above a developmental threshold that is specific for each instar, the speed of development increases linearly with phloem temperature, to optimum temperatures of 30–33°C and decreases sharply at lethal levels above 40°C (Vite, 1952; Annila, 1969; Wermelinger and Seifert, 1998; Baier *et al*., 2007). Population growth rates also peak around 30°C (Wermelinger and Seifert, 1999), which underlines the high potentials of the Eurasian spruce bark beetle for thriving in a warming climate.

The risk of outbreaks may rise with temperature due to more beetles when more generations are completed, especially at higher altitude and latitude where univoltinism is predominant (Austarå *et al*., 1977; Harding and Ravn, 1985; Baier *et al*., 2007). Increasing the number of generations, however, is also linked to higher risks of not completing the generation, resulting in high winter mortality of immature stages. Also, sister broods potentially contribute to population growth (Martinek, 1956; Wermelinger and Seifert, 1999) and are well correlated with specific thermal sums (Annila, 1969; Anderbrant, 1986, 1989). Yet, ceasing thermal limitations will not necessarily lead to unbounded generation development (Faccoli, 2009), as long as the induction of reproductive diapause is controlled by photoperiodic cues (Austarå *et al*., 1977; Schopf, 1989). While juvenile development at the end of the season is not affected, facultative adult diapause is initiated at day lengths below 15 h, unless night temperatures do not become too high, as observed in central European populations of *I. typographus*. The beetles are prevented from swarming due to arrested gonad and flight muscle maturation (Dolezal and Sehnal, 2007), but not from enhanced metabolism, which forces them to resume feeding at temperatures rising above 0°C. Warm winter periods may thus impair the survival of beetles hibernating in the litter without food supply (Koštál *et al*., 2011). Commonly, there is no significant winter mortality of adult imagines due to sub-zero temperatures in central and southern Europe (Faccoli, 2002), as the autumnal changes in day length and temperature progressively promote frost resistance in all instars (Merker and Adlung, 1958; Annila, 1969; Schopf, 1985). The beetle's ability to supercool is enhanced by the accumulation of cryoprotective substances such as sugars and polyols (Koštál *et al*., 2011), lowering lethal temperature thresholds during hibernation to minimum values between –25° and –32°C (Annila, 1969; Hansen *et al*., 1980).

Hence, winter temperatures did not particularly influence the abundance of the Eurasian spruce bark beetle examined for an area extending over south-east and mid-Norway (Økland and Bjørnstad, 2003), while weather patterns and disturbance events played an essential role in the population dynamics and high-distance spatial synchrony of outbreaks (Økland *et al*., 2005). Future spatial and temporal availability of resources are, to a great part, driven by local and regional temperature regimes, which impact the incidence of abiotic disturbances and physiological damages predisposing Norway spruce stands to infestation (Kausrud *et al*., 2012). Future forest mortality due to bark beetles may increase in areas with high abundance of breeding resources and temperature conditions that push the phenology and enhance the populations of *I. typographus*. Several studies unanimously predict bivoltine population development becoming predominant in large parts of northern Europe (Lange *et al*., 2006; Jönsson *et al*., 2007, 2009, 2011), as well as multivoltine populations in central Europe (Baier *et al*., 2007; Hlásny *et al*., 2011; Berec *et al*., 2013) in the course of this century.

11.4 Indirect Effects of Climate Change

11.4.1 Wind

Windstorms are frequently mentioned as a key factor for outbreaks of the Eurasian spruce bark beetle through the past centuries, including records as far back as in the 1600s (Asbjørnsen, 1861; Trägårdh and Butovotisch, 1935; Wellenstein, 1954; Schwerdtfeger, 1955; Christiansen and Bakke, 1989; Schroeder, 2010). Strong winds favour beetle propagation directly by supplying fallen spruces, which are suitable breeding material in the following 1–2 years. Trunks of large spruces are infested more frequently than thin ones, probably due to the preferences for bark thickness of the Eurasian spruce bark beetle (Zumr, 1984; Grünwald, 1986). The risk of wind felling with subsequent attacks of bark beetles are particularly high for the spruces growing near a forest's edge (Peltola, 1996a; Peltonen, 1999; Hedgren *et al*., 2003). The subsequent bark beetle attacks are enhanced by a high proportion of mature spruces in a stand (Becker and Schröter, 2000), as well as a high proportion of mature spruce stands in the landscape (Worrell, 1983). The suitability of individual trees to aggregation and colonization by bark beetles is linked to factors such as tree vigour, nutrient content, defence capacity, sun exposure and shading, drought stress, resistance, etc. (Reid and Robb, 1999; Hedgren and Schroeder, 2004; Wallin and Raffa, 2004; Coops *et al*., 2009; Jakuš *et al*., 2011; Schiebe *et al*., 2012). Also, several studies based on field data have identified factors that make groups of trees and forest stands more predisposed to attacks, such as sun exposure (Jakuš, 1995), drought (Worrell, 1983), soil conditions (Worrell, 1983; Klutsch *et al*., 2009) and forest density (Klutsch *et al*., 2009; Jakuš *et al*., 2011).

After a wind-felling episode, the population size of bark beetles usually builds up over a number of years until it reaches a maximum. The time until peak abundance of bark beetles associated with wind throws depends on the desiccation process of the bark and varies with forest conditions, elevation and latitude (Forster, 1993; Wermelinger *et al*., 1999; Göthlin *et al*., 2000; Schroeder and Lindelöw, 2002), as well as the size of the storm gaps (Schroeder, 2010). There may be interactions between the availability of storm-felled trees and climate (e.g. drought), although no empirical tests have been provided so far. The further development of the beetle population usually shows a marked saw-toothed pattern of fluctuation and a strong negative correlation between the growth rate (R_t) and the population size of the previous year, N_{t-1}, which is typical when resource availability plays a key role in regulating population sizes (Økland and Bjørnstad, 2003; Økland and Berryman, 2004).

Regional differences in the pattern of fluctuations are associated with climatic factors, but the complex direct and indirect influences of different climatic variables imply that the pattern is not correlated strongly with only one single climatic variable (Økland and Bjørnstad, 2003). It is not likely that such differences in fluctuation patterns are determined by inherited differences between regional populations (Mayer *et al*., 2014), since these regions are continuously connected by spruce forest, and the gene flow between these regions must have been considerable during the many centuries since these areas were colonized by this highly dispersive beetle species.

The population development and progress of tree killing is a complex process, presumably set by a bimodal population growth function given by the availability of both windfall and susceptible trees (Økland and Bjørnstad, 2006; Kausrud *et al*., 2011). A large windfall event will increase the beetle population rapidly to a level capable of killing susceptible trees through mass attack coordinated by means of aggregation pheromones. As the breeding material created by the wind felling becomes exhausted or too old for the bark beetles, the main growth of the population will be associated with the colonization of susceptible standing spruces. The epidemic conditions may proceed until the susceptible spruces are exhausted (Økland and Bjørnstad, 2006) or the bark beetles are unable to colonize trees due to sudden changes of extrinsic conditions; for example, the end of favouring weather conditions (see Section 11.4.2). A large windfall event may also cause damage to other trees, and thereby add weakened trees to the reservoir of susceptible spruces that can be colonized by the Eurasian spruce bark beetle (Peltola, 1996a,b; Nielsen, 2001).

More frequent bark beetle outbreaks may be observed if extreme winds become more frequent due to climatic changes (Økland *et al*., 2012). Deep 'low-pressure systems' occur episodically and can lead to extensive wind felling (Benestad, 2005). These large windfall events appear to be a major instigator and synchronizer of bark beetle outbreaks in areas subjected to regionalized weather systems (Økland and Bjørnstad, 2003). Such episodes are relatively rare, but may increase in frequency and severity due to long-termed climatic changes (Carnell and Mitchell, 1996; Kristjansson and Pedersen, 1998; Benestad, 2005; Schlyter *et al*., 2006). Both simulation model results and historical records for the Eurasian spruce bark beetle under Scandinavian conditions demonstrate fairly constant outbreak lengths and highly variable waiting time between outbreaks due to the irregular occurrence of strong storms (Økland and Bjørnstad, 2006). According to model simulations, a long-term increase of windfall frequency is expected to result in more frequent outbreaks of shorter durations (Økland *et al*., 2012).

The role of wind felling for outbreaks of the Eurasian spruce bark beetle is probably linked to other system-specific factors, such as hydrological conditions, productivity of spruce forests and beetles and exposure to strong storms. For example, the mean population sizes of the Eurasian spruce bark beetle are decreasing towards northern latitudes (Økland and Bjørnstad, 2003). Even though strong storms occur in the extensive spruce forests of northern Scandinavia and Finland, this region has been spared from major bark beetle outbreaks so far. Low beetle productivity at northern latitudes may have been an important factor for this, but the productivity of the northern beetle populations may increase with a climate change. Southern Scandinavia has experienced huge outbreaks when wind-felling storms have coincided with periods of high temperatures and drought stress (Worrell, 1983). In central Europe, some storms may trigger extensive bark beetle outbreaks without a predisposing period of heat and drought, such as the ongoing outbreak in the High Tatra Mountains that started after the storm in 2004 (Nikolov, 2012). In the southern distribution area of the Eurasian spruce bark beetle, the outbreaks appear to be linked to drought rather than episodes of wind felling (Marini *et al*., 2012).

11.4.2 Drought

Outbreaks of the Eurasian spruce bark beetle have long been associated with drought stress of Norway spruce as a result of site conditions constraining the water supply of the trees (Merker, 1952; Schwerdtfeger, 1955; Bakke, 1983; Worrell, 1983; Christiansen and Bakke, 1988). Due to shallow rooting systems, Norway spruce stands are particularly vulnerable to low amounts of precipitation, as well as to water deficiency in upper soil layers (Schwerdtfeger, 1955; Schmidt-Vogt, 1989). Hence, various models developed for evaluating the probability of infestation by *I. typographus* consider soil and hydrological variables such as the soil depth, drainage class and available water capacity of the soil as important predictors (Dutilleul *et al*., 2000; Netherer and Nopp-Mayr, 2005; Ogris and Jurc, 2010; Overbeck and Schmidt, 2012). Climate extremes can aggravate the effects due to bad matches of site conditions and tree species composition, and may impact the associated forest insects significantly; as, for example, observed during the heat and drought wave in Western Europe in 2003 (Rouault *et al*., 2006). Exceptionally dry seasons potentially increase the risk of epidemics, although the effects of water stress on tree susceptibility are often difficult to distinguish from the positive influence of high temperatures on beetle propagation (Christiansen and Bakke, 1997). Water deficit during spring and summer was identified as a driver for bark beetle outbreaks in European conifer forests in analyses of disturbance data on both local and large scales (Dobbertin *et al*., 2007; Seidl *et al*., 2011b). The correlation of drought periods and *I. typographus* population dynamics was also demonstrated by recent studies at the southern margins of the distribution of Norway spruce (Faccoli, 2009; Marini *et al*., 2012) and in southern Sweden (Marini *et al*., 2013).

Regarding tree level, it may not be easy to find evidence of drought-induced changes in disposition to bark beetle attack. Physiological responses of potential hosts depend on their primary vitality status and on the intensity and duration of drought episodes (Huberty and Denno, 2004). Moderate water stress commonly enhances the synthesis of carbon-based secondary metabolites and of constitutive resin flow (Lombardero *et al*., 2000), and has been shown to increase resistance to bark beetle-associated fungi (Christiansen and Glosli, 1996; Desprez-Loustau *et al*., 2006). Severe drought stress, on the other hand, may limit oleoresin production and impair plant water transport due to native embolisms, potentially increasing host susceptibility for scolytid attack (McDowell *et al*., 2008; Jactel *et al*., 2012b). It can be assumed that implications of stand water deficiency are highly variable, depending on tree and scolytid species. For example, water deficiency of trees indicated by highly negative twig water potentials (Lu *et al*., 1995) was linked to the improved boring and breeding success of the southern pine beetle, *Dendroctonus frontalis* (Lorio *et al*., 1995), but this parameter did not explain fully the differences in infestation by the pine shoot beetle, *Tomicus destruens* (Branco *et al*., 2010).

Some studies based on controlled attacks by the Eurasian spruce bark beetle indicate the high suitability of fairly vigorous host trees (Baier, 1996; Baier *et al*., 2002), but others find that the beetle density necessary for tree killing, referred to as 'the epidemic threshold', is strongly related to tree vigour (Mulock and Christiansen, 1986). Recently, Netherer *et al*. (2015) provided empirical evidence for reduced Norway spruce resistance to *I. typographus* under water-limiting conditions, yet accompanied by declining host acceptance with extreme drought stress.

The projected intensification of drought events for parts of Europe calls for a better understanding of the effects on the Eurasian spruce bark beetle and its tree host (Lindner *et al*., 2010), especially for forest sites that already suffer from water deficit and will be affected most negatively by increasingly stressful climatic conditions (Netherer and Schopf, 2010; Ogris and Jurc, 2010; Seidl *et al*., 2011b). For example, choice experiments on differentially drought-impaired trees (Turcani and Nakladal, 2007) might contribute to a better understanding of how water supply acting upon constitutive and inducible defences (Rosner and Hannrup, 2004; Franceschi *et al*., 2005) affects attack and propagation rates.

11.4.3 Interactions

Interactions with natural enemies

A variety of insect predators and parasitoids are associated with the Eurasian spruce bark beetle; yet, there is no clear evidence for an effective control of populations by antagonists (Kenis *et al*., 2004; Marini *et al*., 2013). Natural regulation is influenced by antagonist and bark beetle population densities, species-specific rates of parasitism or consumption (voracity), habitat and extra food resources, synchronization between antagonist and bark beetle life stages, and by the outbreak phase (Wermelinger, 2002; Wermelinger *et al*., 2012). Natural enemies show the highest impact at the time that scolytid populations build up and decline, respectively (Wermelinger, 2002). Even ravenous subcortical predators, such as the highly abundant larvae of *Thanasimus formicarius* (larvae), were observed to be most effective at lower prey densities (Mills, 1985; Kenis *et al*., 2004). The seasonal importance of antagonistic species can fluctuate significantly. While predators were dominant in the first study year of an outbreak, parasitism appeared as the main cause for the collapse of bark beetle survival in the following year (Wermelinger, 2002). In contrast to generalist predators that respond quickly to new food supply, many specialized parasitoids tend to show delayed responses to changes in host densities (Wermelinger, 2002; Bouget and Duelli, 2004). However, in a long-term study from Sweden, the predator density did not emerge as an important prey-regulating factor in the population dynamics of the Eurasian spruce bark beetle (Marini *et al*., 2013).

Silvicultural practices as well as abiotic disturbance events shape forest composition and structure, thereby influencing the supply of microhabitats for xylophagous and saproxylic insects (Bouget and Duelli, 2004; Wermelinger, 2004). While the retention of dead wood and the presence of mainly small and highly structured gaps support the availability of niches for predators and parasitoids (Bouget and Duelli, 2004), more catastrophic storms due to climate change may implicate explosive beetle propagation uncoupled from natural regulation. Strong fragmentation of habitats potentially reduces the efficiency of parasitoids, which may, on the other hand, be more mobile than many predators (Weslien and Schroeder, 1999).

Natural enemies are guided to their prey mainly by host tree volatiles and bark beetle pheromones (Mills, 1985; Kenis *et al*., 2004; Wermelinger, 2004). Changes in the vitality or decay status of host trees indicated by characteristic assemblages of monoterpenes are perceived not only by the scolytids but also by their antagonists. *T. formicarius* is, for instance, highly attracted to ipsdienol and ipsenol, while hymenopteran species respond to semiochemicals signalling the optimal bark beetle development stage for parasitism (Hulcr *et al*., 2006). Despite these strong olfactory cues, synchronization of life cycles might be disturbed by rising temperatures due to changes in emergence patterns (Wermelinger *et al*., 2012). For example, parasitoids that commonly overwinter as (pre)pupae in bark beetle host galleries (Kenis *et al*., 2004) emerged in higher proportion in the autumn of warm years (Wermelinger *et al*., 2012). Similar to their scolytid prey, antagonists also react on increased temperature sums by accelerated development and earlier flight (Mills, 1985; Wermelinger *et al*., 2012), but do not necessarily follow the increased growth rates of the bark beetle (Feicht, 2006). Low winter temperatures probably lead to similar high mortality rates among pre-imagines of *I. typographus* and hibernating larvae of natural enemies (e.g. predatory flies of the genus *Medetera*) (Faccoli, 2002; Kenis *et al*., 2004), but there is no information about the effects of warmer winters on antagonist survival or diapause patterns. Based on a 4-year study from Switzerland, Wermelinger *et al*. (2012) suggested that rising temperatures might even reduce bark beetle winter survival due to fungal diseases and enhanced predation.

Interactions with other bark beetles

Many bark beetle species show fairly high niche overlap with the Eurasian spruce bark beetle (Ringsgård, 1975; Zumr, 1984; Grünwald, 1986). Only in Scandinavia, 23 species with spruce as a principal host are sympatric with the Eurasian spruce bark beetle (Lekander *et al.*, 1977). All of these species are much less aggressive than the Eurasian spruce bark beetle and are strongly inferior in interaction with this species.

Climate change may play a role in modifying the interactions between the Eurasian spruce bark beetle and other bark beetle species. For example, higher frequency of wind-felling episodes may make the inferior species less dependent on a high niche overlap with the Eurasian spruce bark beetle for survival, while inferior species with little niche overlap tend to become extinct locally when the probability of wind felling is low (Økland *et al.*, 2009). Some bark beetles co-occurring on spruce in Europe may occasionally contribute to tree killing. The double-spined bark beetle (*Ips duplicatus* Sahlb.), the six-spined spruce bark beetle (*Pityogenes chalcographus* L.), the small spruce bark beetle (*Polygraphus poligraphus* L.) and the smaller eight-toothed spruce bark beetle (*Ips amitinus* Eichh.) can kill trees or contribute to killing trees. Tree-killing behaviour of these species has been observed in association with outbreaks of the Eurasian spruce bark beetle (Knižek, 2001; Mihalciuc *et al.*, 2001; Novotny *et al.*, 2002; Jurc and Bojović, 2004). The outbreaks of these species are infrequent and modest today (Lekander *et al.*, 1977; Grégoire and Evans, 2004; Hedgren, 2004), but their tree killing may be more frequent as an indirect effect if climate change promotes more outbreaks by the Eurasian spruce bark beetle.

The strongest positive interactions are expected when both bark beetle species are strongly ‘aggressive’ (Økland *et al.*, 2009). This may lead to escape from control by competition, and increase the frequency of outbreaks of tree killing. This situation might occur if the spruce beetle, *Dendroctonus rufipennis* (Kirby), should become established in Europe. Model simulations of hypothetical interactions of the spruce beetle and the Eurasian spruce bark beetle indicated that interspecies facilitations could result in more frequent and severe outbreaks than those caused by the Eurasian spruce bark beetle alone (Økland *et al.*, 2011). More drought-stressed and wind-felled forests in a future climate may increase the likelihood of the spruce beetle to become established in Europe. Furthermore, climate change may have an effect on the geographical range in Europe that is most suitable to synchronize facilitated attacks of both bark beetle species.

11.4.4 Host-tree distribution, vigour and bark beetle outbreaks

There may be significant regional differences in the future conditions for the Eurasian spruce bark beetle. Global warming is expected to change the conditions for the regeneration of Norway spruce towards the north and higher elevation in Europe (Langvall, 2011). Along with a warmer climate, the limit where epidemic populations can be reached may be moved towards the north and into the extensive areas of the north European spruce forest that so far have been spared from bark beetle outbreaks (Økland *et al.*, 2007). In the southern and lower end of the current distribution, the spruce forests may experience suboptimal and stressful conditions and intensified outbreaks due to loss of tree vigour. In this part, the strategies of tree planting and management may be important for the outcome of future bark beetle outbreaks. The changes in forest structure and composition associated with management activities such as promoting conifers and increasing standing timber volume strongly influence susceptibility to bark beetle attacks (Seidl *et al.*, 2009, 2011a,c; Jactel *et al.*, 2012a). In particular, Seidl *et al.* (2011c) showed that forest changes contributed in the same order of magnitude as climate change to the increase in disturbance damage across European forests. Changes in forest extent, structure and composition particularly affected the variation in wind and bark beetle damages. Although these continental analyses have provided interesting general patterns, they also indicated that different parts of Europe could respond to global change differently due to different local forest management and general climate.

Northern Europe

In the boreal forests of northern Europe, coniferous forests constitute a large portion of the terrestrial land, e.g. 43.0% in Fennoscandia (Global Forest Resources Assessment, 2010). These forests are periodically subjected to large storms and wind-felling episodes that may trigger bark beetle outbreaks (Økland and Bjørnstad, 2003; Marini *et al*., 2013), and analyses of climate model results indicate that the frequency of such storms may increase in the future (Benestad, 2005). In addition to storm frequency, the extent of bark beetle outbreaks is dependent on the management and structure of northern forests in the future. The reported damage from storms seems to have increased during the past century (Nilsson *et al*., 2004; Seidl *et al*., 2011c), due mostly to the propagation of spruce plantations with forest structure characterized by tall trees with superficial root systems (Puhe, 2003; Jactel *et al*., 2012a). An increase in the annual probability of large windfall episodes is expected to result in immediate declines in both outbreak lengths and waiting time between outbreaks (Økland and Bjørnstad, 2006), but the availability of weakened and storm-damaged trees is certainly a factor of how long the outbreaks will last and the further development of bark beetle populations (Komonen *et al*., 2011).

Climate warming is expected to be relatively stronger in northern high latitudes (Serreze and Francis, 2006). The interactions between climate warming and future bark beetle outbreaks are complex. There is little evidence of the direct effects of temperature and drought on population growth in the few time-series studies available from Scandinavia, except for some effect of summer drought in the southernmost part (Økland and Berryman, 2004; Marini *et al*., 2013). A positive effect of temperature has been found in a short-term study (Bakke, 1992), and Worrell (1983) has reported that bark beetle attacks are most frequent in Norwegian forests with poor and steep soil that are particularly predisposed to drought. According to Jönsson *et al*. (2012), the lack of the clear effect of temperature may indicate that warmer temperatures can have both positive and negative density feedbacks on population dynamics, depending on the availability of storm-felled trees. A warmer climate is expected to give a northern expansion of the area experiencing two generations per year (Lange *et al*., 2006; Jönsson *et al*., 2009), which may possibly allow the Eurasian spruce bark beetle to exploit the available breeding material more efficiently than with one generation.

There are indirect effects of temperature that may be important for the development of bark beetle population sizes and future outbreaks in the north. The Eurasian bark beetle may benefit from the decline and dieback of Norway spruce, which has been observed in many places in Europe, including southern Scandinavia. Norway spruce is relatively sensitive to drought (Karlsson *et al*., 1997; Wallin *et al*., 2002; Allen *et al*., 2010), and drought stress has already been shown to be a limiting factor for the growth of Norway spruce in parts of south Norway (Solberg, 2004; Andreassen *et al*., 2006).

Forest productivity decreases with latitude, and this decrease is coupled with the production of host substrates (dead spruce). The average population size of the Eurasian spruce bark beetle in a 24-year-long time series from more than 100 localities showed a linear decrease with increasing latitude in Scandinavia (Fig. 11.2). In northern areas, global warming may increase the productivity of host trees, and indirectly the beetle populations, due to more access to breeding substrates and enhanced conditions for flight and attacks. There have been few occurrences of bark beetle outbreaks in the extensive areas of spruce forest in the northern part of the Nordic countries, but these areas may be subject to huge outbreaks if a warmer climate increases the population sizes of the Eurasian spruce bark beetle due to indirect effects (Økland *et al*., 2007). For example, the population sizes estimated by

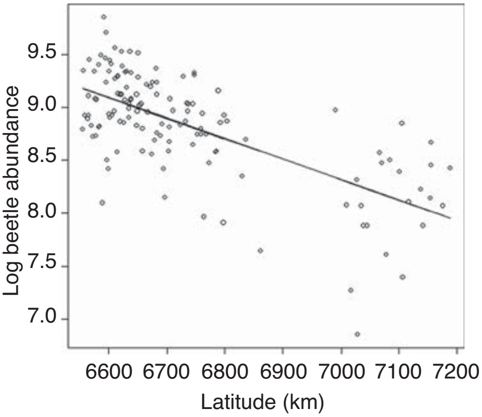

Fig. 11.2. Mean log abundance of *Ips typographus* of municipalities in Norway plotted against latitude. (From: Økland and Bjørnstad, 2003.)

monitoring traps in the northern spruce areas of Norway (Trøndelag and Nordland) multiplied several times, and local infestations were observed in the warm period from 2002 to 2009. In southern Sweden, there were large bark beetle populations, two generations per year, and spruce killing in the warm summers after the huge windfelling episode, 'Gudrun', in 2005. In southeastern and southern Finland, the damage by the spruce bark beetle increased alarmingly in the warm years of 2010 and 2011.

Other parts of Europe

The spruce forests of central and Western Europe contain a large proportion of artificial plantations. In these areas, the large propagation of pure artificial forests, often in climatic conditions outside the natural range of spruce, has created stands that are potentially highly susceptible to bark beetle attacks (Marini *et al.*, 2012). Under these conditions, increasing stand age is a further key risk factor, together with other abiotic triggers such as drought or the availability of storm-felled trees (Lausch *et al.*, 2011). Some mountain regions of central Europe, such as the High Tatra Mountains in Slovakia, experience frequent storm-felling of spruces that trigger extensive outbreaks of the Eurasian spruce bark beetle (Nikolov *et al.*, 2014).

At least at the southern margin of the spruce distribution in Europe, lower-than-average precipitation seems generally to favour infestations by the Eurasian spruce bark beetle (Wermelinger, 2004; Rouault *et al.*, 2006; Faccoli, 2009; Marini *et al.*, 2012). Spruce trees at low altitudes and latitudes actually grow substantially faster than in the zones where spruce has occurred historically. This is consistent with the hypothesis that spruces in forests located in warm climates have increased growth but reduced defences against bark beetles (Baier *et al.*, 2002).

While large windfall events are considered a major trigger of bark beetle outbreaks in northern Europe (Økland and Bjørnstad, 2006; Schroeder, 2007), these extreme climatic events may have relatively less importance in some of the southern regions where there is a lower frequency and extent of wind-felling episodes (but see Gilbert *et al.*, 2005; Nikolov *et al.*, 2014). In flat and easily accessible forest areas, the negative effects of storms can be partially mitigated by the quick removal of fallen trees by foresters. None the less, storms may become more important in the future if climate change results in more windfall events that overwhelm the capacity for sanitation responses by foresters (Marini *et al.*, 2012).

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12 Pine Wood Nematode, Pine Wilt Disease, Vector Beetle and Pine Tree: How a Multiplayer System Could Reply to Climate Change

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Abstract

The pine wood nematode, *Bursaphelenchus xylophilus*, constitutes a major threat to pine forests across the world. Under climatic conditions favourable to the expression of the pine wilt disease caused by the nematode, susceptible pine trees may die within a few months following nematode inoculation. Although considered a secondary pest in its native North America, this organism has caused huge damage in areas it has invaded in south-eastern Asia and south-western Europe. The nematode is carried by local long-horned beetles in the genus *Monochamus*, which vector it to pine trees first during maturation feeding and then when ovipositing. As climate is an important driver of insect vectors, nematodes and disease expression, we explore in this chapter how a changing climate could affect this multiplayer system in the future. Warming up is effectively susceptible to enlarging vector distribution, to accelerating its development and possibly to enhancing its flight performances. Therefore, it could change the time window of nematode transmission and increase the spread rate of the nematode. Other factors such as humidity, windthrows and forest fires could also affect vector population dynamics. Simultaneously, climate warming is likely to increase the development rate and reproduction of the nematode, and thus the nematode population growth. Finally, the expression of pine wilt disease is also modulated by warm temperatures and water deficit, causing drought stress to pine trees. With temperature increase, areas at risk of the disease would probably extend. Actually, pine wilt disease has recently been observed to expand its range in areas of eastern Asia that were previously considered as unsuitable. Modelling the disease spread helps to assess more precisely the potential effects of climate change and to evaluate the potential economic impacts.

12.1 Introduction

The pine wood nematode, *Bursaphelenchus xylophilus*, is at present a major threat to pine forests across the world (Suzuki, 2002; Webster and Mota, 2008; Vicente *et al*., 2012). When introduced in a healthy tree,

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such nematodes spread rapidly through the vascular system and resin canals, and block water conductance in the xylem (Vicente *et al.*, 2012). As a result, tree physiological processes are disrupted, leading to a rapid wilt of the pine needles and to tree death in less than 3 months (Kuroda, 2008). This tree decline, called ‘pine wilt disease’, has already caused the death of millions of trees in Japan (Mamiya, 1984) and China (Zhao, 2008), and more recently of thousands of trees in Portugal (Rodrigues, 2008). The economic impact is incredibly high in terms of damage, contingency plans and embargoes (Bergdahl, 1988; Dwinell, 1997; Shin, 2008), and could be worse in the future in case of further spread of the pine wood nematode (Økland *et al.*, 2010; Bergseng *et al.*; 2012; Soliman *et al.*, 2012).

B. xylophilus is native to North America (Dropkin *et al.*, 1981). Originally isolated from a wood sample of longleaf pine (*Pinus palustris*) in Louisiana in 1929 (Steiner and Buhrer, 1934), its causal relationship to pine wilt disease was only assessed 50 years later, when the nematode was identified as being responsible for the death of an Austrian pine (*Pinus nigra*) introduced in Missouri (Dropkin *et al.*, 1981). Indeed, the pine wood nematode is considered there as a secondary pest of stressed or recently dead trees because native North American pines appear generally more resistant to the pine wilt disease than exotic ones (Wingfield *et al.*, 1982; Bergdahl, 1988; Evans *et al.*, 1996). Unfortunately, from the beginning of the 20th century, *B. xylophilus* was introduced successively into a number of Eurasian countries hosting *Pinus* species with which the nematode did not co-evolve. It appeared in Japan in 1905 (Yano, 1913), then it invaded other eastern Asian countries during the 1980s (China, 1982, Cheng *et al.*, 1986; Korea, 1988, Yi *et al.*, 1989; and Taiwan, 1995, Chang *et al.*, 1995), and it was finally introduced into Europe during the late 1990s and early 2000s (continental Portugal, 1999, Mota *et al.*, 1999; western Spain, 2008, Robertson *et al.*, 2011; and Madeira island, 2009, Fonseca *et al.*, 2012). In these invaded areas, pine wilt disease can express in healthy trees infested by the pine wood nematode under two conditions: (i) the infested tree is susceptible to pine wilt disease; and (ii) environmental conditions are favourable for disease development (Evans *et al.*, 1996).

Thus, understanding and predicting the spread of the pine wood nematode and that of pine wilt disease is very important to define the best control measures. However, it is a real challenge because the underlying mechanisms of dispersal and disease expression are relatively complex. Sousa *et al.* (2011) established that a direct wood-to-wood transmission of the nematode was very hypothetical. Indeed, wherever it is, either in native or invaded areas, the pine wood nematode is vectored only by long-horned beetles (Coleoptera: Cerambycidae) in the genus *Monochamus* (Linit, 1988), although it is possibly carried by other insects that remain unable to transmit it to the trees (Kobayashi *et al.*, 1984; Linit, 1988). Up to 200,000 nematodes may be carried by a single beetle as it emerges from an infested host tree (Fielding and Evans, 1996). Potential *Monochamus* vectors are present in most world regions, and new associations between pine wood nematode and native beetle species have appeared immediately in all the areas invaded by the nematode; for example, with *Monochamus alternatus*, *Monochamus saltuarius* and *Monochamus galloprovincialis* in Eurasia (Evans *et al.*, 1996; Akbulut and Stamps, 2012). Indeed, the relationships appear beneficial to both partners in these areas. When an adult long-horned beetle introduces nematodes in a healthy tree during its maturation feeding, the trees subsequently weakened by the nematode activity become favourable to oviposition by sexually mature female beetles searching for declining hosts (Togashi *et al.*, 2004). Additional nematodes can be transmitted through oviposition scars, but in a much lower proportion than during maturation feeding (Mamiya, 1984). Figure 12.1 illustrates this highly synergic cycle, which is likely to trigger the population dynamics of the beetle in nematode-infested areas. Although remarkable similarities in life traits are observed among the vector *Monochamus* species, minor differences

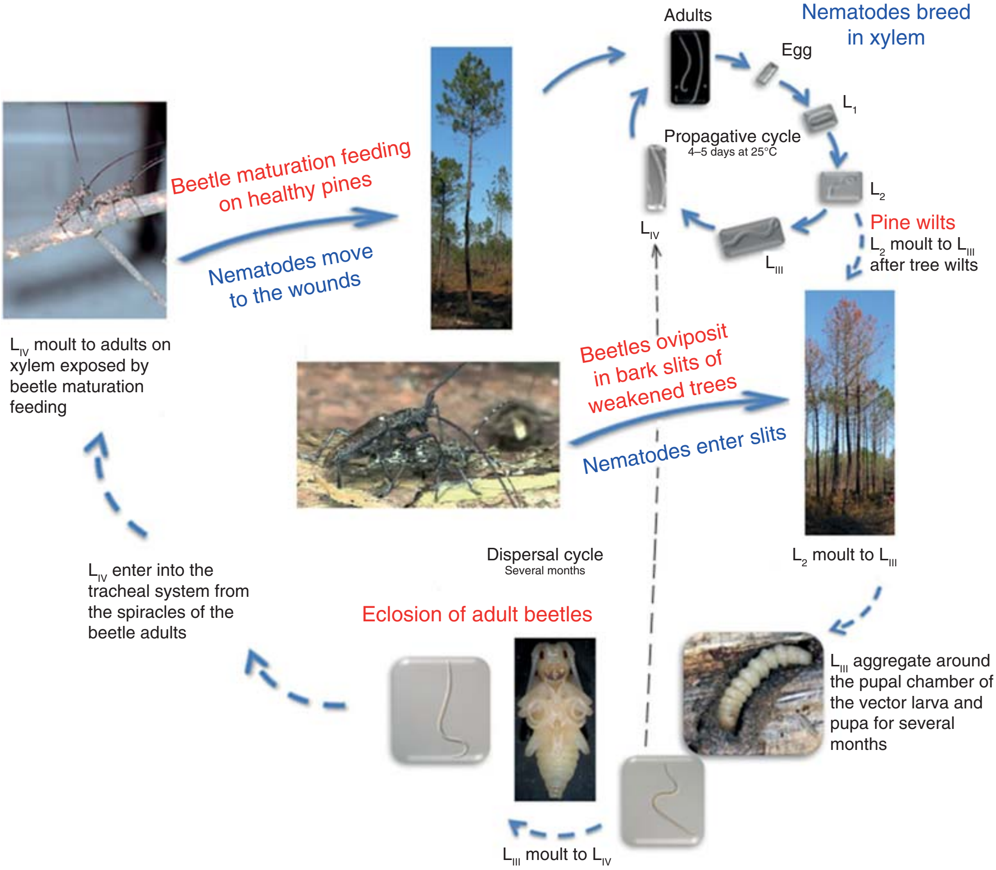

Fig. 12.1. Synergic life cycles of long-horned beetles, *Monochamus* spp., and pine wood nematodes, *Bursaphelenchus xylophilus*. Solid lines represent the nematode propagative developmental pathway; dashed lines show the dispersal pathway. Under favourable conditions, animals go through direct development (L_1–L_4) to the reproductive adult . *B. xylophilus* has two different dispersal and long-lived stages, including the dispersal third larval stage (L_{III}) and the dispersal fourth larval stage (L_{IV}). Moulting to L_{III} is induced environmentally by deteriorating conditions in the pine tree, but moulting to L_{IV} is dependent on the presence of an emerging *Monochamus* adult beetle. Although L_{III} typically moults to L_{IV}, if L_{III} are exposed to favourable conditions, they can resume reproductive development, moulting into L_4 larvae and then adults.

exist, especially in the thermal thresholds for the development stages and in voltinism (Akbulut and Stamps, 2012), which can modulate their response to climate change.

Besides, pine wood nematode survival and development is known to be influenced by climatic factors such as temperature and humidity (Panesar *et al.*, 1994). Moreover, the susceptibility of tree species can also vary across areas, whereas environmental conditions can favour or prevent disease expression. Thus, pine wilt disease has been observed mainly in areas where the mean daily summer temperatures exceed 20°C for several weeks (Rutherford and Webster, 1987; Rutherford *et al.*, 1990; Pérez *et al.*, 2008), whereas it has not been observed in regions with colder weather, although the nematode can survive severe cold and drought (Mamiya, 1984). Evans *et al.* (2008)

have shown that both seasonal drought and high temperatures causing water deficit drive potential tree evaporation and the tree's defence capability against the pine wood nematode, and play an important role in disease development. Warmer summer temperatures are thus likely to trigger disease expression in new areas. Recent records of pine wilt disease in areas showing cold climates that were previously not supposed to be at risk in Japan (Nakamura *et al*., 2013) and China (Huang *et al*., 2013) led to the assumption that climate change was already effective in allowing such a process.

Therefore, climate warming (+1.8 to +4°C predicted between 1980–1999 and 2090–2099; Meehl *et al*., 2007) could have substantial effects on the spread of the disease (Webster and Mota, 2008) by affecting specifically, as well as in a combined way, the different compartments of this multiplayer system: nematode survival and growth, carrier beetle distribution, tree susceptibility and disease expression. Besides favouring the natural expansion of pine wood nematodes from the invaded areas, climate change might also influence directly the likelihood of nematode establishment, as well as disease expression, into remote territories following long-distance, human-mediated movements with wood trade of both insect vector and nematode, such as is observed for other invasive species (Walther *et al*., 2009).

In this chapter, we will review successively the potential effects of climate change on the different partners of this complex system, and then detail the existing spread models and their predictions for pine wilt disease according to the scenarios for climate change in the coming years.

12.2 Response of Monochamus Vector Beetles to Climate Change

A total of 112 species are presently recognized in the subgenus *Monochamus* of the long-horned beetle genus *Monochamus* (World Catalog of Lamiinae Cerambycids, 2013). Commonly known as sawyer beetles or sawyers, because their larvae bore into dead or dying trees, especially conifers, they include species native to Palearctic and Neartic regions, and to Africa. Most species in Eurasia and North America are developing mainly in *Pinus*, but some may utilize *Picea* and *Abies* species as well (Akbulut and Stamps, 2012; Wallin *et al*., 2013). Potential *Monochamus* vectors are thus present throughout the world wherever there are native pine species. At least nine of these beetles have yet been proved to be capable of transmitting pine wood nematodes. In the native North American range of *B. xylophilus*, Akbulut and Stamps (2012) have listed four *Monochamus* species as vectors (the Carolina pine sawyer – *M. carolinensis*; the white-spotted sawyer – *M. scutellatus*; the southern pine sawyer – *M. titillator*; and the spotted pine sawyer – *M. mutator*), whereas three more species (*M. marmoratus*, *M. notatus* and *M. obtusus*) have been reported as carriers, but it is not known yet whether they can actually transmit the nematode to the trees' vectors. In the areas invaded by the nematode, new associations have arisen with *M.* species native to these regions. In eastern Asia, four species have been identified as vectors: the Japanese pine sawyer, *M. alternatus*, in Japan and China, the Sakhalin pine sawyer, *M. saltuarius*, in Japan and Korea, and *M. nitens* and *M. urussovi* both in Japan (Akbulut and Stamps, 2012). Among the six species known to occur in Europe, only *M. galloprovincialis* has so far been proven to act as a vector in the Iberian Peninsula and Madeira, but there is no indication that the other species (*M. sutor*, *M. sartor*, *M. saltuarius*, *M. urussovi* and *M. impluviatus*) cannot function as vectors if the nematode spreads to areas where they occur, the more as all of them can develop in pines, at least occasionally (Wallin *et al*., 2013).

Monochamus beetles developing in pine species share largely similar biological and behavioural patterns (Akbulut and Stamps, 2012), although minor differences in life histories can be noticed (e.g. development in branches for *M. galloprovincialis* conversely to other species in the trunk; Koutroumpa *et al*., 2013). The similarity especially concerns their intimate association with pine wood nematode, which has largely been documented in *M. carolinensis* (Linit, 1988), *M. alternatus* (Mamiya, 1984; Zhao *et al.*, 2007, 2013a), *M. saltuarius* (Jikumaru and Togashi, 2001) and *M. galloprovincialis* (Naves *et al.*, 2006, 2007a). Whereas adult beetles emerge from the dead pines in which they developed, their maturation feeding occurs necessarily on healthy trees. If a beetle is infested by pine wood nematode, nematodes are transmitted mostly to the tree during this phase, through feeding wounds in the bark (Linit, 1990; Naves *et al.*, 2007a; Zhao *et al.*, 2007). Subsequent nematode activity rapidly results in a decline of the infested tree, which then becomes attractive to sexually mature *Monochamus* looking for mating and ovipositing sites in weakened trees. Early-instar beetle larvae first feed under the bark, and then bore galleries in the sapwood and heartwood. Overwintering usually occurs as a larva. Mature larvae form pupal chambers in the outer xylem. In *Bursaphelenchus*-infested trees, nematodes aggregate in these pupal chambers (Zhao *et al.*, 2007) and finally enter the tracheae of the adult beetle about to emerge (Yang *et al.*, 2003). Emerging beetles then disperse and carry the nematodes to other pine trees where they feed. The nematodes then exit the beetle trachea and enter the feeding wounds. This synergic interaction is thus providing oviposition resources for *Monochamus*, triggering its population dynamics in infested areas (Linit, 1988; Yang *et al.*, 2003).

As with the range of many other insect species developing under temperate latitudes, the distribution of *Monochamus* species is constrained by thermal barriers, especially by low winter temperatures that regulate the survival of the overwintering larvae. It has been especially documented in *M. alternatus* (Ma *et al.*, 2006; Tian *et al.*, 2008), whose distribution range in China appears to be more restricted than that of its host trees (Ning *et al.*, 2004). Based on the values of the supercooling points of the different development stages, Ma *et al.* (2006) suggested the −10°C isotherm for January air temperature to be considered as the northern potential limit of the beetle's range in China and proposed to identify a potential dispersal region between the −10° and −4°C isotherms, temperatures above this latter value being highly suitable to the overwintering fifth-instar larvae. Moreover, Tian *et al.* (2008) has shown that the larvae's supercooling point has a bimodal distribution that may correspond to a bet-hedging strategy that allows survival in unexpected cold snaps. In Japan, the northern limit of *M. alternatus*'s distribution range was assumed to be 40°N (Kobayashi *et al.*, 1984). Thus, a latitudinal shift of winter isotherms with global warming is likely to allow *M. alternatus* to expand to regions not yet colonized, as has already been observed for a number of other insect species (Robinet and Roques, 2010). Besides natural expansion, such a shift is likely to facilitate the establishment of beetles transported a long distance with infested wood packaging material, especially from the economically well-developed east coast of China westwards to the less-developed interior. Hu *et al.* (2013) established the presence of such non-local *Monochamus* populations in several sites newly infested by the nematode.

However, thermal barriers other than winter temperatures are additionally shaping the species' range. A minimal threshold allowing female oviposition has been assessed at 21.3°C for mean air temperature during summer (Kobayashi *et al.*, 1984). Thus, in both China and Japan, too low temperatures during summer led to the conclusion that several areas located below the northern potential limit, such as Hokkaido (Kobayashi *et al.*, 1984), Tibet and central Yunnan (Ma *et al.*, 2006), had, until now, been unsuitable for beetle establishment. However, an increase in summer temperatures may also remove this barrier. Conversely, higher temperatures during summer may have adverse effects on the vector. In *M. galloprovincialis*, the rate of larval development decreased above 30°C, and a lethal upper threshold was estimated to occur between 32 and 35°C (Naves and Sousa, 2009), but a recent survey revealed that the beetle was widely distributed all over the Portuguese territory, although large microclimatic differences might exist between areas (Petersen-Silva *et al.*, 2014).

Beetle development is also likely to be sped up by warmer temperatures in spring, summer and autumn. However, a major striking difference between *Monochamus* species is the potential number of generations per year and the associated occurrence of an obligatory larval diapause. The North American *M. carolinensis* has only a facultative diapause (Linit, 1985) and can complete two generations per year when the climate is favourable, such as in the southern USA (Pershing and Linit, 1986). By contrast, most of the *Monochamus* species of the invaded areas present in the last larval instar an obligatory diapause, which terminates by midwinter; i.e. in *M. alternatus* (Togashi, 1991, 1995), *M. saltuarius* (Jikumaru *et al.*, 1994) and *M. galloprovincialis* (Naves *et al.*, 2007b; Koutroumpa *et al.*, 2008). Although the induction period has not yet been identified precisely, this diapause thus usually prevents the occurrence in these species of a second generation during late summer or autumn (records of several generations per year for *M. alternatus* in tropical southern China need confirmation; Wang, 1992), even if larval development will be sped up by warmer temperatures. Therefore, in Eurasia, the entire cycle is completed in 1 year, or 2 years if the conditions are unfavourable. In Europe, the percentage of 2-year development in *M. galloprovincialis* varies along a latitudinal gradient from 5% in Portugal (Naves *et al.*, 2007b) and 8% in north-central France (Koutroumpa *et al.*, 2008) to 90% in southern Finland (Tomminen, 1993). The lower development threshold for post-diapausing larvae varies from 10.1°C for *M. saltuarius* (Jikumaru and Togashi, 1996) to 12.2°C for *M. galloprovincialis* (Naves and Sousa, 2009). In the latter species, the development rate appears to be related linearly to temperatures between 15 and 30°C (Fig. 12.2). Warming in spring and summer is thus likely to accelerate development, with a possible earlier occurrence of adult emergences and flights, but a major consequence might be a significant increase in the proportion of insects developing in 1 year at higher latitudes instead of in 2 years.

Warmer temperatures in late spring and summer may also affect flight performances and adult dispersal positively. Togashi *et al.* (1993) noticed that the flight period of *M. alternatus* was limited by low temperatures in areas with cold climates, shortening the oviposition period. However, studies aimed at assessing flight performances rarely took into account the response to temperature variations (Akbulut and Linit, 1999; David *et al.*, 2014). Indirect studies based on temperature records during trappings and release–recapture experiments produced contrasting results. Recaptures of *M. galloprovincialis* adults by Hernández *et al.* (2011) were not correlated directly to temperatures in Spain, but Vincent (2007) observed that the number of adults trapped in different regions of France was increased significantly by higher temperatures.

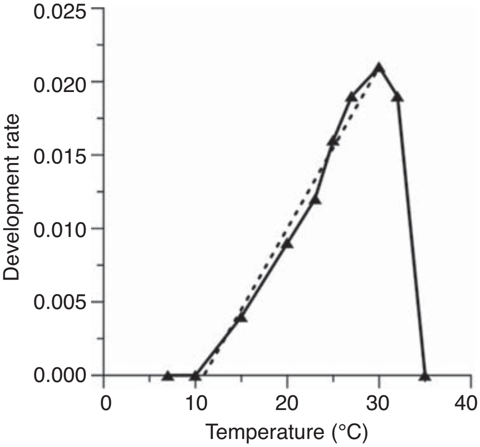

Fig. 12.2. Developmental response (mean development per day) to constant temperatures of post-diapausing larvae of *Monochamus galloprovincialis*. The dashed line corresponds to the best linear fit between 10°C and 30°C ($R^2 = 0.983$). (Modified from Naves and Sousa, 2009.)

Climate variables other than temperature increase are likely to affect vector expansion and dynamics, but they remain little documented. Kong *et al.* (2006) pointed out the importance of relative humidity to the longevity of adult *M. alternatus*, which was significantly longer under 90% RH than that at 40% RH when the temperature was 25°C. In a congeneric species attacking coffee trees in Africa, the coffee white stem borer (*M. leuconotus*), the precipitation-related variables were more important in determining the species range than the temperature-related ones (Kutywayo *et al*., 2013). Climatic events resulting in windthrows as well as in forest fires are providing resources for development in the absence of the nematode; for example, for *M. scutellatus* in North America (Gandhi *et al*., 2007; Bélanger *et al*., 2013). Thus, the predicted higher frequency of climate anomalies may also trigger the population dynamics of *Monochamus* spp.

12.3 Response of Pine Wood Nematode to Climate Change and Potential Changes in Pine Wilt Disease Expression

The intimate, mutualistic relationships between *B. xylophilus* and *Monochamus* spp. have been largely detailed during recent years (Zhao *et al*., 2013a,b, 2014; see Fig. 12.1). *B. xylophilus* has two different dispersal and long-lived stages, including the dispersal third-larval stage (L_{III}) and the dispersal fourth-larval stage (L_{IV}) (Dwinell, 1997). L_{III} aggregation and L_{IV} formation are specifically coordinated with the life cycle of the vector beetle. Aggregation of the L_{III} larvae around the beetle's pupal chamber is induced by specific ratios of volatile terpenes (α-pinene, β-pinene and longifolene at 1:2.7:1.1) produced by *Monochamus* as it matures (Zhao *et al*., 2007). Then, the formation of the dispersal L_{IV} stage is specifically induced by the secretion of long-chain C16 and C18 fatty acid ethyl esters (FAEEs) in large amounts on the *Monochamus* body surface during eclosion, possibly by modulating the conserved insulin/IGF-1 and DAF-12 signalling pathways (Zhao *et al*., 2013a). The L_{IV} can then enter the tracheal system of the adult beetle for dispersal to a new pine tree.

Several factors influence the occurrence and distribution of pine wood nematodes and pine wilt disease, including climate conditions and biointeractions with vector beetles, fungal species and host tree species. Temperatures directly affect the development rate of *B. xylophilus*. The nematodes complete their life cycle within 4–5 days at 25°C and within only 3 days at 30°C (Mamiya, 1975). However, high temperatures could have negative effects on nematode development (above 28°C) and on nematode reproduction (above 35°C) (Mamiya, 1975; Takemoto, 2008). Besides, in China, the number of trees killed by the nematode each year was correlated positively to the number of nematodes present in *M. alternatus* pupal chambers and to the population densities of the beetles (Zhao *et al*., 2013b). In addition, Ophiostomatoid fungi identified in dead trees positively influenced the reproduction of the pine wood nematode and its interactions with host pine trees (Maehara, 2008; Maehara and Futai, 2000; Niu *et al*., 2012). This is especially true for two species isolated in Japan and China, *Ophiostoma minus* and *Sporothrix* sp. 1, which were shown to influence nematode reproduction strongly and positively, and consequently the number of nematodes dispersed by the beetles (Maehara and Futai, 2000; Zhao *et al*., 2013b, 2014).

The potential consequences of climate change are related mostly to increased seasonal drought stress and warmer temperatures during summer. Water deficits together with high temperatures increased tree susceptibility and favoured pathogen and vector development in Japan and North America (Rutherford and Webster, 1987; Evans *et al*., 2008). It has been known for some time that where the mean July temperature is less than 20°C, the disease is rare, even though the pathogen may be present (Rutherford and Webster, 1987). In Japan, most infestations occurred in areas over 22°C (Sturrock *et al*., 2011). To determine areas at risk, it is thus possible not only to consider temperature thresholds but also host tree susceptibility, as some *Pinus* species are more susceptible than others (Evans *et al*., 1996). Depending on the combination between these two factors, a risk level can be calculated. Most of the forest stands in north-western Spain are facing a high risk, and this could be worse in the case of climate warming (Pérez *et al*., 2008). This risk is probably underscored, as this approach does not consider other factors that may emphasize the development of the disease. In China, disease occurrence and severity are correlated positively with annual mean temperature and winter and spring precipitation, but correlated negatively with June precipitation (Xi and Niu, 2008; Zhao, 2008). Relative humidity is also an important factor influencing areas infested with pine wilt disease. Too much precipitation in spring and winter led to a serious epidemic situation in Dinghai district. The more precipitation in June, the lighter the epidemic situation is. Relative humidity is prevalent from March to May, being correlated positively with epidemic degrees (Xi and Niu, 2008). At present, a large part of south-eastern China is favourable to nematode establishment. With a 3°C warming, the suitable area could expand by 40%, especially in the northern and northwestern regions, but the Tibetan Plateau and the surrounding mountainous area, and also the northern part of Yunnan and the western part of Sichuan, would remain quite unfavourable (Fig. 12.3; Robinet *et al*., 2009).

Although the invaded eastern Asian countries have made enormous efforts to eradicate the pine nematode, in 2012 pine wilt disease was found in unexpected regions of Japan (Aomori Prefecture; Nakamura *et al*., 2013), South Korea (Boryeong, Chungnam province, on *Pinus densiflora*; Yangju, Gyeonggi province, on *Pinus koraiensis*) and northern China (Shanxi and Henan provinces on *Pinus tabulaeformis*; Huang *et al*., 2013; Shinya *et al*., 2013). It is strongly suspected that these newly colonized territories have become suitable for both nematode establishment and disease expression as a consequence of recent climate change.

12.4 Model Predictions for the Expansion of Pine Wilt Disease with Future Climate Change

To determine the most appropriate control measures, it is important to understand the spread mechanism of the nematode and the wilt disease, and anticipate where they could spread in the future. Using mathematical models to simulate the potential spread of the nematode and of the disease's development can help us to predict the areas at risk, and consequently the areas where surveillance should be intensified.

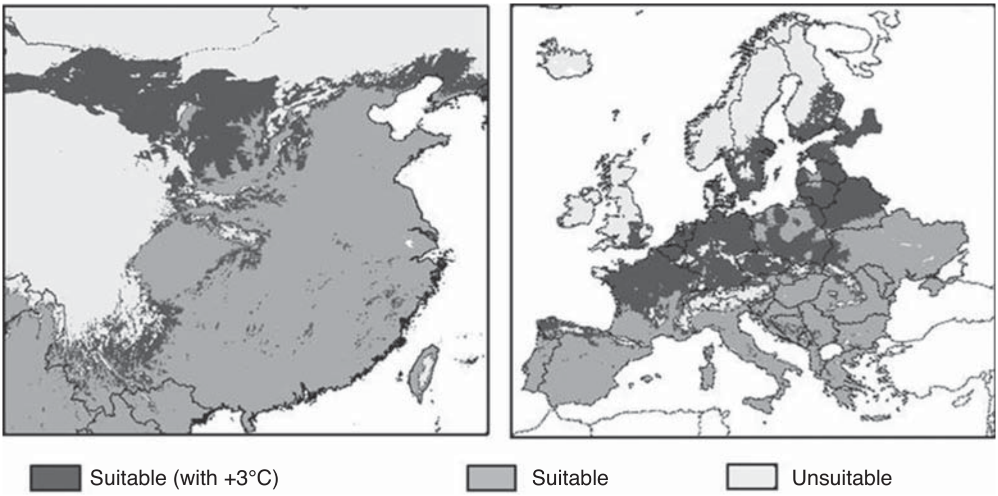

Fig. 12.3. Area potentially suitable for disease expression under the current climate and under a hypothetical 3°C temperature rise in China and Europe based on the following temperature thresholds: mean temperature in July above 21.3°C and mean temperature in January above –10°C in China, and mean temperature in July above 20°C in Europe (Modified from Robinet *et al*., 2009, 2011).

Some generic spread models have recently been developed to assess the risk of invasion by plant pests, and the pine wood nematode was used as a particular case study (Robinet *et al.*, 2012; Pukkala *et al.*, 2014). These models require a limited number of parameters and they have been designed in such a way that it is not necessary to have extensive mathematical knowledge to use them. Consequently, they are very useful for a preliminary assessment, especially when time, data availability and mathematical expertise are limited. However, for the pine wood nematode, some specific and more detailed mathematical models have been developed, describing more precisely not only the growth and dispersal mechanisms but also the disease development.

A specific spread model was developed to describe the change in insect vector density and healthy tree density in time and space (Yoshimura *et al.*, 1999; Takasu *et al.*, 2000; Togashi and Shigesada, 2006; Takasu, 2009). This model was fitted to the pine wood nematode invasion in Japan and considered flight performance and life traits of the local vector, *M. alternatus*. This model does not describe explicitly the spread of the pine wood nematode. It assumes that all adult vectors bear the nematodes, that they have a given probability to transmit them to host trees and, once infested by the nematodes, the host trees necessarily die and are therefore suitable for female vector oviposition. As it was designed to be applied at the scale of a pine stand (small scale), it considers neither long-distance dispersal resulting from accidental transportation of infested material nor variability in disease expression. The results of this model suggest that there is a pine density threshold and a vector density threshold below which the pine wood nematode fails to establish (Yoshimura *et al.*, 1999). This kind of Allee effect arises from the mutualism between the nematode and its vector: the nematode transmitted by the vector to the tree makes the tree suitable for vector oviposition, and in turn, the vector emerging from this tree can further disseminate the nematode (Takasu, 2009). Allee effects could potentially work in favour of successful eradication. However, in countries where the disease symptoms are not yet expected to occur, such as northern Europe, it would not be possible to eradicate the nematode under reasonable conditions (with less than 10,000 samples/year and a radius for the clear cut-zone of less than 8 km) (Økland *et al.*, 2010).

Another model was developed to describe the spread of pine wilt disease symptoms at a larger spatial scale. It was initially fitted to the history of invasion in China (Robinet *et al.*, 2009), where the insect vector was mainly *M. alternatus*, as in Japan. The advantage of this model was that it was applied at a large scale and it simulated not only short-distance dispersal due to vector active flight but also the possibility of long-distance dispersal due to human activity. In China, long-distance dispersal appeared to be very important, representing more than 90% of the new infestations at an average distance of 111–339 km from the likely source populations (Robinet *et al.*, 2009). The best factor that could explain these long-distance jumps was human population density. This factor probably gave a good indication of the magnitude of human activity across the country, and thus an indication of the amount of imports of wooden (potentially infested) materials.

This model was later applied to Europe in order to determine the European ports from which the nematode and wilt disease could spread the most rapidly, and thus where surveillance should be targeted more carefully (Robinet *et al.*, 2011). Since very little information is known about the invasion in the Iberian Peninsula so far, this model was applied to Europe to give a first indication of the invasion risk. However, caution was needed in interpreting the results because the model was calibrated on the invasion in China and should be adjusted to the European features of invasion. For instance, the vector species observed respectively in the Iberian Peninsula (*M. galloprovincialis*) and in China (*M. alternatus*) present some biological differences (e.g. larval development in branches versus trunk), and the flight performances may differ. Climate constraints considered in the model were not the same for China as for Europe. In China, the insect vector is not present throughout the country, and its distribution is limited by both summer and winter temperatures (mean temperature in July above 21.3°C and mean temperature in January above –10°C; cf. Section 12.2). In Europe, the large distribution of the insect vector should not be a constraint on the spread of the nematode. The only temperature constraint considered in the model applied to Europe is the temperature threshold for disease expression (mean temperature in July above 20°C; Rutherford and Webster, 1987), which is less restrictive than the temperature constraints used in China for the Asian vector. From the simulations of this model, climate change could affect the spread of pine wilt disease in Europe more strongly than in China (Robinet *et al*., 2011). With 3°C of temperature rise, the area suitable for disease expression could expand by 40% in China against more than 100% in Europe (Robinet *et al*., 2011) (Fig. 12.3). In fact, elevated mountains in western China would act as a barrier to wilt disease, even in the case of a high temperature increase, whereas such a barrier would not exist in Europe. Depending on the climate change scenario and the port where the nematode may escape, pine wilt disease could spread over 8–34% of European territory by 2030 (Robinet *et al*., 2011). Direct economic impacts resulting from the wood loss caused by nematode spread from Portugal could be particularly high in Portugal, Spain, Italy and France by 2030 if the nematode is not controlled (Soliman *et al*., 2012). The total economic impact including reduction in the domestic supply of industrial round wood and its consequence on the domestic market price would be very high, with large economic consequences on the European conifer forestry industry.

The main key factors that need to be studied carefully to describe the potential spread of pine wilt disease accurately are: the dispersal capability of the insect vector, which is not the same in Asia and Europe; human accidental transportation of infested materials; and the conditions for disease development. These factors are currently being studied in the EU project, REPHRAME (http://www.forestry.gov.uk/fr/rephrame), and data should be available very soon that will help us to refine the spread model in Europe. In the context of climate change, the crucial component of the spread model is the condition for disease expression. The temperature threshold of 20°C given in the past (Rutherford and Webster, 1987) provided a good overview of what could happen. However, this condition is a little too simplistic to describe precisely the complex physiological tree processes that lead to tree death. Describing these processes with an evapotranspiration model helps to determine the conditions that lead to tree wilt, such as tree resistance level and the day of nematode inoculation (Evans *et al*., 2008; Gruffudd *et al*., 2013). With higher temperatures, some parts of Europe could become suitable for disease expression and tree death could occur more rapidly in regions where the disease can currently develop (Gruffudd *et al*., 2013).

Beyond all these biological and physiological factors, another important factor to consider when assessing the likelihood of pine wilt disease spread is obviously the control measures applied by the national authorities, and their efficiency.

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13

Northern Geometrids and Climate Change: From Abiotic Factors to Trophic Interactions

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Abstract

The subarctic mountain birch forests have been periodically disturbed by geometrid moth outbreaks since at least the mid-19th century. The effects of these disturbances can be seen from landscape-level dieback of the birch forest to local-level changes in soil processes. Recent research efforts have demonstrated that the geometrid moth–birch forest system is undergoing changes that could be linked to the ongoing climate warming. Milder winter and spring temperatures influence winter survival and outbreak ranges of the moths, and are also alleviating range expansions and the spread of new species to the area. Moreover, phenology matching with the host plant may be altered. The outcome appears to be intensified outbreaks and a potential for altered species interactions and dynamics with ecosystem-wide consequences.

This chapter will first introduce the prevailing dynamics of the mountain birch–geometrid system and the reported ecosystem effects of geometrid outbreaks. Second, the chapter summarizes observations of ongoing abiotic changes in the area and presents the potential known and unknown effects on the study species. Finally, the chapter discusses the future scenarios for this northern ecosystem and the possibility of major ecosystem changes.

13.1 Introduction

Climate change at northern latitudes is expected to result in altered temperatures, particularly during the winter season (Oldenborgh *et al*., 2013). For northern ectotherms, this means changes in abiotic conditions during the most critical stages of their life cycles, namely overwintering and the onset of the short growing season. The direct effects of these changes could include higher survival rates during winter, improved matching phenology with the host plant for more optimal development and dispersal and establishment to areas previously unattainable for the insect herbivore (Bale *et al*., 2002). Particularly regarding insects with pest status, improved abiotic conditions may lead to more severe or prevalent outbreaks. Furthermore, the direct changes in one or more species within one ecosystem inevitably result in changes in the interactions and may cause trophic cascades within the system (Berggren *et al*., 2009; Post *et al*., 2009).

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The response of an ecosystem to individual changes depends on the strength and number of species interactions. Resource limitation and generally simple food webs with a small number of species interactions characterize arctic and subarctic ecosystems. In more species-rich systems, the existing biodiversity might buffer against the effects of climate change and sustain ecosystem stability (Tilman *et al*., 2006; Haddad *et al*., 2011; Post, 2013). In northern ecosystems, the role of individual species, species interactions and their responses to climate change play a pronounced role in ecosystem stability (Post *et al*., 2009).

In northern Fennoscandia, the dominant subarctic mountain birch forests have been disturbed periodically by geometrid moth outbreaks as far back as historical records go (Tenow, 1972). Severe moth outbreaks may kill vast areas of forests and have ecosystem-wide effects, from tree layer productivity to soil nutrient cycling and carbon balance (Jepsen *et al*., 2013; Karlsen *et al*., 2013). Despite the massive damage, the birch ecosystem recovers on most occasions. However, prior to resolving all the particularities of this intriguing system of cyclic outbreaks, changes are occurring in the system that could be linked to ongoing climate warming.

13.2 Climate Change and Ecosystem Stability in the Fennoscandian Birch Forest

Regional climate scenarios predict pronounced effects of global warming for northern latitudes. The increase in mean temperatures has been observed and is predicted to be more pronounced during winter months than summer months. A median increase of 4.3°C for northern Europe for December–February was predicted by Christensen *et al*. in 2007 (Lindner *et al*., 2008), and predictions ranging from an increase of 2 to 7.5°C by 2100 have been presented in the 5th Assessment for the International Panel for Climate Change (Oldenborgh *et al*., 2013). In particular, a decreasing global trend in cold events has been observed (Hartmann *et al*., 2013; Oldenborgh *et al*., 2013). In subarctic ecosystems, cold climatic conditions and short growing season are the most limiting abiotic factors defining current species distribution and composition. Climate change is expected to affect directly the winter survival of insects (Bale *et al*., 2002; Bale and Hayward, 2010), species distribution ranges (Parmesan *et al*., 2005; Burrows *et al*., 2014) and phenology matching between herbivorous insect and the host plant (Bale *et al*., 2002; Singer and Parmesan, 2010). Climatic-driven changes in these factors may lead to abrupt changes in northern ecosystems.

A changing climate may affect different trophic levels in dissimilar ways. The magnitude and timing of responses may also differ between trophic levels (Berggren *et al*., 2009). Furthermore, changes in one trophic level are bound to cascade through the ecosystem, potentially disturbing ecosystem stability, particularly in highly connected systems such as the subarctic forest ecosystem. In addition, the strength of species interactions in a system may change and eventually lead to loss of biodiversity, even though species richness itself might not be altered (Ings *et al*., 2009). Even seemingly stable systems may have alternative dynamical states that the ecosystem may be shifted to after new disturbances (Holling, 1973; Scheffer *et al*., 2009). Small changes in the system caused directly or indirectly by climate change may thus be detrimental for the system (Post *et al*., 2009).

13.2.1 The mountain birch forest ecosystem

The subarctic birch forest of northern Fennoscandia is dominated by mono- or polycormic mountain birch (*Betula pubescens* ssp. *cerepanovii* (Orlova) Hämet-ahti) and spans more than 10° latitude (59°–71°N) along the Scandes mountain chain. The mountain birch forests cover a climatic gradient from mild and moist oceanic regions in north-west Norway, through cold and dry continental areas in northern Sweden and

Finland to the Kola Peninsula. Geometrid outbreaks occur throughout these unmanaged and fairly undisturbed forests at decadal intervals, but vary greatly in amplitude and spatial extent. Ranging from the local phenomenon of partly defoliated trees to hundreds of square kilometres of completely leafless forests (Tenow, 1972; Kallio and Lehtonen, 1973; Lehtonen and Heikkinen, 1995; Jepsen *et al*., 2009), the geometrid outbreaks affect the whole ecosystem, from changes in tree chemistry and morphology (Ruohomäki *et al*., 1997; Kaitaniemi *et al*., 1999; Huttunen *et al*., 2012), through ground-layer vegetation (Jepsen *et al*., 2013; Karlsen *et al*., 2013) to cascading effects on other trophic levels (see Section 13.3.2). Historically however, the mountain birch ecosystem appears to have had a high resilience towards the disturbance caused by geometrid outbreaks, perhaps due to the long cycle period between the moth outbreaks and the nutrient storing and regeneration ability of the mountain birches. Global warming, however, provides an all-new challenge for the mountain birch forests and the northern ecosystem.

13.3 Birch Forest Geometrids in Northern Fennoscandia

13.3.1 Distribution, life history and outbreak dynamics

Geometrid outbreaks are by far the most important natural disturbance factor in the mountain birch forest in northern Fennoscandia. Three species in particular occur in high densities and cause severe defoliation (Fig. 13.1): the autumnal moth (*Epirrita autumnata* Borkhausen), the winter moth (*Operophtera brumata* Linnaeus) and the scarce umber moth (*Agriopis aurantiaria* Hübner). Of these, *E. autumnata* has been present in the system for at least as far back as historical records go. This species has a more or less circumpolar distribution, but outbreaks have been reported mainly from northern Fennoscandia (Tenow, 1972). *O. brumata* is an ‘old invader’ in northern Fennoscandia, first recorded in coastal regions as far north as 70°N in the 1890s (Tenow, 1972). Its native distribution has been restricted to Europe and Asia, where it is considered an important economic pest in fruit orchards and mainly oak forests (Tenow *et al*., 2013). *O. brumata* has been introduced into North America quite recently, in both eastern and western parts, where it is regarded as an invasive pest species due to the expanding distribution and outbreak range (Elkinton *et al*., 2010). *A. aurantiaria* is a new invader in northern Fennoscandia. It was first recorded in coastal regions at 69°N in 1991 (K. Ruohomäki, 2014, personal communication), and since then has become established as a serious pest, along with *O. brumata* and *E. autumnata*, in coastal northwest Norway (Tenow *et al*., 2007; Jepsen *et al*., 2011). The species is known to occur at outbreak densities in deciduous forests in southern and eastern Europe.

All the above-mentioned geometrids have similar univoltine life cycles. The overwintering eggs are highly cold tolerant, and endure temperatures as low as from –31°C

Fig. 13.1. Larvae of (a) *Epirrita autumnata*, (b) *Operophtera brumata* and (c) *Agriopis aurantiaria*. (Photograph courtesy of Moritz Klinghardt.)

to −36°C during the diapause stage depending on species (see Section 13.4.1). The eggs hatch in the spring in synchrony with the dominating deciduous tree species in the area, the mountain birch (see Section 13.4.1). Although the larvae of all these species feed mainly on birch in northern Fennoscandia, they are reported to utilize a large number of host species throughout their ranges, and none of them can be considered a birch specialist. During mass occurrences, most canopy-forming woody species present in the birch forest (including *Salix* spp. and *Sorbus aucuparia*), as well as a number of dwarf shrubs (*Betula nana*, *Vaccinium myrtillus* and occasionally *Vaccinium uligonosum*), may be defoliated by the larvae.

E. autumnata and *A. aurantiaria* feed freely on the leaves, whereas the larvae of *O. brumata* tend to feed inside the buds in early spring or to spin the leaf loosely together and feed sheltered. The larval period lasts from mid/late May through June, through five instars. The overall duration of the larval period is affected by a combination of food plant quality and temperature (Haukioja and Niemelä, 1974; Ayres *et al*., 1987; Virtanen and Neuvonen, 1999; Ammunét *et al*., 2011). During the larval stages, all the resources needed for maturation and reproduction are acquired (Tammaru and Haukioja, 1996; Tammaru *et al*., 1996). Thus, fecundity is directly dependent on the attained resources during the larval stage (Haukioja *et al*., 1988; Tammaru *et al*., 1996; Klemola *et al*., 2004, 2007, 2008). The pupae are formed in the cover of soil and moss in late June/early July. Temperature affects pupal size and development in a non-linear way, with maximal development rate and pupal size at intermediate temperatures (Peterson and Nilssen, 1996, 1998; Heisswolf *et al*., 2009; but see Holliday, 1983). The long pupal period is followed by adult eclosion in the autumn, with much variation in the eclosion dates. The females of *O. brumata* and *A. aurantiaria* are wingless (or nearly wingless), whereas the females of *E. autumnata* have wings, but probably only fly short distances. The adults mate and females lay eggs on tree branches, preferring lichen and the crevices of bark as the surface for egg laying.

Northern populations of both *E. autumnata* and *O. brumata* are known to exhibit cyclic population dynamics, with recurring density peaks every 9–11 years (Tenow, 1972; Ruohomäki *et al*., 2000). Accumulating evidence suggests that the outbreak dynamics of *A. aurantiaria* can be expected to be similar to the other two species (Jepsen *et al*., 2011). A combination of factors is probably affecting the reoccurring cycles (Ruohomäki *et al*., 2000; Haukioja, 2003). Studies on the role of parasitoids in the cyclic dynamics indicate that the combination of factors shaping the dynamics also varies on spatial (coastal–continental) and temporal scales (Ruohomäki, 1994; Bylund, 1999; Klemola *et al*., 2002, 2010, 2014; Schott *et al*., 2010). The outbreaks are frequently synchronous over fairly large geographical areas (Klemola *et al*., 2006). However, where both *O. brumata* and *E. autumnata* occur, the peak density of *O. brumata* often lags 1–3 years behind the peak density of *E. autumnata* (Tenow *et al*., 2007; Klemola *et al*., 2008).

13.3.2 Effects of outbreaks on the ecosystem

Periodic moth outbreaks have implications for both ecosystem structure and functioning in the subarctic birch forests of Fennoscandia. Defoliators usually do not kill their host immediately but inflict damage that accumulates over several years and results in elevated tree mortality, often in interaction with other stressors (Hicke *et al*., 2012). This presents a challenge in any effort to assess the ecosystem consequences of moth outbreaks. Severe moth outbreaks can cause close to complete defoliation of birch stands (Tenow, 1972; Kallio and Lehtonen, 1973), inflicting extensive stem mortality (Tenow and Bylund, 2000; Jepsen *et al*., 2013) and growth reduction for years following an outbreak (Hoogesteger and Karlsson, 1992). However, the predominantly polycormic growth forms of the mountain birch possess a well-developed ability to resprout from the old root system (Kallio and Mäkinen, 1978; Tenow *et al*., 2004). Hence, outbreaks can play an important role in forest rejuvenation (Lehtonen and Heikkinen, 1995; Tenow *et al*., 2004). Interactions with mammalian herbivores will ultimately determine the successional trajectory of the forest following moth outbreaks. Semi-domestic reindeer are numerous in northern Fennoscandia – approximately 590,000 in Sweden, Norway and Finland (CAFF, 2010) – and they utilize the birch forest to a seasonally varying degree depending on geography and herding regime (Suominen and Olofsson, 2000; Forbes and Kumpula, 2009). High grazing pressure can retard or prevent the regeneration of the forest, thus potentially driving a vegetation state transition from continuous forest to open savannah-like woodland or treeless tundra. Previously forested areas in Finnish Lapland have been left treeless after the 1960s outbreak, presumably due to high-intensity grazing and browsing by reindeer (Lehtonen and Heikkinen, 1995; Oksanen *et al*., 1995).

Following regional-scale outbreaks in the 1960s, a number of descriptive studies (Tenow, 1972; Kallio and Lehtonen, 1973; Lehtonen and Yli-Rekola, 1979) have documented changes in forest floor vegetation, in addition to tree layer changes. Since then, significant advances in our understanding of the role of understorey plants, in particular ericoid dwarf shrubs, in the integrity and productivity of northern forest ecosystems have been made (Tybirk *et al*., 2000; Nilsson and Wardle, 2005; Nordin *et al*., 2009; Jonsson and Wardle, 2010; Manninen *et al*., 2011). Following the regional outbreaks in the 2000s, drastic vegetation state changes in the understorey layer have been documented: most noticeably, a shift from dwarf shrub-dominated (in particular *Empetrum nigrum*) towards grass-dominated (*Avenella flexuosa*) communities (Jepsen *et al*., 2013; Karlsen *et al*., 2013). Excess nitrogen from larval frass and decomposing larvae, in addition to the loss of the allelopathic *E. nigrum*, have implications for ecosystem productivity and below-ground resource dynamics (Kaukonen *et al*., 2013), which still await exploration.

Severe moth outbreaks alter the resource availability for a number of consumer species. Cascading impacts of the increase in grasses and the loss of dwarf shrubs on mammalian herbivores have been demonstrated (Jepsen *et al*., 2013). While moth larvae in outbreak years may provide insectivorous species with an ephemeral pulse of overabundant resources, general habitat degradation can be expected for many species over time, due to adverse changes in resource availability. Further, the accumulation of dead wood can provide a resource pulse for saproxylic and fungivorous insects over time (Palm, 1959; Vindstad *et al*., 2014).

13.4 Birch Forest Geometrids in a Changing Climate

The climate influences every stage of development in geometrids. The predicted warming in the north is expected, especially during the winter season, with an overall increase in average temperature and a decrease in cold events. Therefore, two developmental stages in geometrids are particularly relevant in the context of climate change: the level of cold tolerance in the overwintering egg stage, influencing winter survival, and the temperature requirements for egg hatching in spring, determining the level of phenology matching with the host plant, and consequently the amount of attained resources.

13.4.1 Climate controls of geometrid dynamics

The overwintering moth eggs prepare for the coming winter by producing chemicals that protect them from freezing. The potential to tolerate cold temperatures increases as the eggs enter the diapause stage (September–November) (Nilssen and Tenow, 1990) and reaches maximum potential in November, well before the coldest winter periods occur (Nilssen and Tenow, 1990). The achieved maximum cold tolerance remains unaffected by short warm spells until embryogenesis in February–March (Nilssen and Tenow, 1990). During the diapause stage, the eggs of *E. autumnata* and *O. brumata* can tolerate temperatures as low as –36.8°C and –36.3°C, respectively (Nilssen and Tenow, 1990; Ammunét *et al*., 2012). In comparison, the eggs of the more southern and coastal *A. aurantiaria* are able to tolerate a minimum temperature of –31°C (Ammunét *et al*., 2012). At the onset of embryogenesis, the cold tolerance of the *E. autumnata* eggs decreases to about –30°C (Nilssen and Tenow, 1990). Details on cold tolerance during embryogenesis of *O. brumata* and *A. aurantiaria* are less known. However, similar decreases of 5–7°C in cold tolerance compared to diapause cold tolerance are likely for at least *O. brumata* (Ammunét *et al*., 2012). At any one stage during overwintering, temperatures below the level of cold tolerance of the eggs may induce egg mortality, and thus serve either to reduce the population levels the following spring or to protect cold regions entirely from geometrid outbreaks (Tammaru *et al*., 1996; Virtanen *et al*., 1998; Neuvonen *et al*., 1999). However, most of continental northern Fennoscandia has experienced a strong decreasing trend in the frequency of sufficiently cold days to induce egg mortality (Fig. 13.2).

Once the eggs approach embryogenesis, the incubation time required for egg hatching is short, which allows a rapid response to the onset of spring (Nilssen and Tenow, 1990). As is the case for many forest insect pests, the success of the spring-feeding geometrid larvae depends on maintaining close phenological synchrony with budburst in the host plant (van Asch and Visser, 2007). Disrupted synchrony caused by increasing spring temperatures was demonstrated in oak-feeding *O. brumata* populations further south following late 20th century warming (Visser and Holleman, 2001). Intriguingly, it

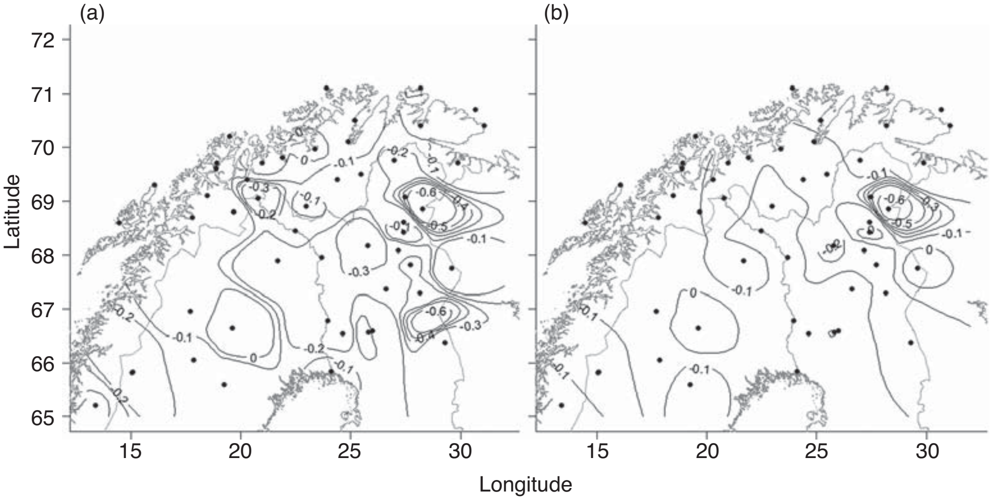

Fig. 13.2. The trend in the total number of winter (1 December to 30 April) days with an average temperature below –31°C (a) and –36°C (b) per year for the period 1950–2009. The two temperature thresholds used were chosen to illustrate the differences in cold tolerance between *Agriopis aurantiaria* (–31°C) and *Operophtera brumata*/*Epirrita autumnata* (–36°C). The linear regression between the number of days below the temperature threshold and the year was calculated based on daily mean temperatures for each meteorological station (black points) and interpolated between stations to create isoclines using kriging. Negative values indicate a decrease in the number of days below threshold temperatures, while values close to zero indicate no change during the period in question. Daily temperature data were obtained from the Finnish Meteorological Institute (FMI Open Data), the Norwegian Meteorological Institute (www.eklima.no, met.no) and the Swedish Meteorological and Hydrological Institute (SMHI).

has been shown since then that the egg hatching dates of *O. brumata* in that system have gone through genetic changes in response to the altered selection pressure, resulting in renewed phenological match between egg hatching and host budburst (van Asch *et al*., 2013). The short growing season in northern Fennoscandia promotes a rapid onset of spring, where budburst may occur within days of snowmelt. Rapid foliage development in the mountain birches leads to an equally rapid deterioration of the leaves as food for newly hatched geometrid larvae (Haukioja *et al*., 1978; Ayres and MacLean, 1987), and it is reasonable to believe that the egg hatching dates of the geometrids in the north will be under strong selection pressure similar to what has been shown for oak-feeding *O. brumata* further south. So far, this is a topic that has been little explored for birch forest geometrids, but it is known that the three species differ in their warmth sum requirements for egg hatching (Jepsen *et al*., 2011). *E. autumnata* eggs hatch at lower accumulated temperatures than the two more southern geometrids, *O. brumata* and *A. aurantiaria*. While the hatching of *E. autumnata* and *O. brumata* seem to match the leaf budburst of the mountain birch fairly accurately, despite their differences in temperature requirements, *A. aurantiaria* seems to suffer from a greater mismatch with the host plant phenology. However, with increasing incubation temperatures, *A. aurantiaria* has been shown to hatch in increasing synchrony with both *O. brumata* and birch budburst (Jepsen *et al*., 2011). Given a continuation of the marked increase in the frequency of spring days with temperatures above zero across northern Fennoscandia (Fig. 13.3), an increasing match with host plant phenology is likely for this species.

13.4.2 Climate-driven range expansions

More benign climatic conditions provide opportunities for the spread of new species as the restricting abiotic conditions, especially during winter and spring, become less restraining (Parmesan *et al*., 1999; Walther *et al*., 2002; Jepsen *et al*., 2011). Many northern European lepidopteran species, for example, have expanded their boundaries northward by tens to hundreds of kilometres (Parmesan *et al*., 1999; Parmesan, 2006). Such range expansions and invasions of novel species may alter the prevailing interactions within the native system (Parmesan, 2006; Tylianakis *et al*., 2008; Kenis *et al*., 2009).

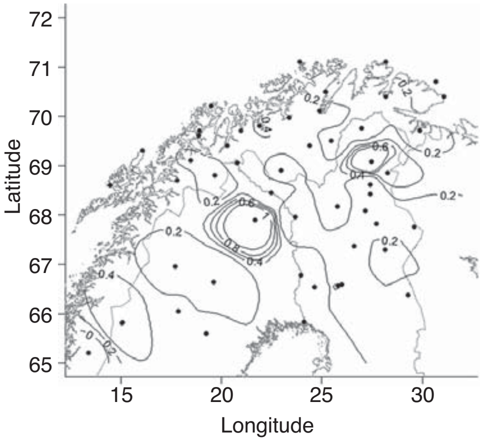

Fig. 13.3. The trend in the total number of spring (1 January to 31 May) days with an average temperature above 0°C for the period 1950–2009. The linear regression between the number of days above 0°C and year was calculated based on daily mean temperatures for each meteorological station (black points) and interpolated between stations to create isoclines using kriging. Positive values indicate an increase in the number of days where eggs can accumulate above-zero temperature sum required for hatching. Values close to zero indicate no change in the number of days with above-zero temperatures during the period in question. (From temperature data as in Fig. 13.2.)

Simultaneously with the decreasing trend in cold events during the winter (Fig. 13.2; Jepsen *et al*., 2008; Ammunét *et al*., 2012) and an increase in warm spring days (Fig. 13.3), both *E. autumnata* and *O. brumata* have expanded their outbreak ranges in northern Fennoscandia (Jepsen *et al*., 2008, 2011). *E. autumnata*, which has been responsible for outbreaks across the region for centuries, has expanded its outbreak range during these most recent decades to include also the coldest, most continental regions (Fig. 13.4a). *O. brumata* outbreaks, which were formerly restricted to coastal mountain birch forest (Tenow, 1972), have expanded steadily northwards and inland towards the more continental and colder areas (Fig. 13.4b). Apart from localized outbreaks in the 1960s in north-west Finnmark and northern Sweden, the first region-wide outbreak by *O. brumata* occurred in the mid- to late 2000s, reaching all the way to the low-arctic tundra in north-east Norway. In the most recent years (2012 and 2013), *O. brumata* have been recorded as far inland as near the Norwegian–Finnish border near Kilpisjärvi in northern Finland, and for the first time attained outbreak densities in the Abisko valley in northern Sweden (Ammunét and Bylund, personal observation). The aforementioned invasion by *A. aurantiaria* appears to be restricted so far to climatically mild coastal regions in Norway (Fig. 13.4c).

13.4.3 Ecosystem consequences

Increased temperatures during the winter and spring seasons have already allowed defoliators to expand their outbreak range in the northern mountain birch forests. In theory, the geographical variation covered by the northern mountain birch forests and the persisting temporal heterogeneity of the host tree–insect ecosystem indicate that the mountain birch forests should be fairly resistant against disturbances such as the invasion of new species. Systems with temporal heterogeneity in general have been argued to be able to sustain more competing species than less heterogeneous systems (Melbourne *et al.*, 2007), and therefore to be more resistant against invasive species that may influence the ecosystem. However, the climate change-driven species range expansion has not only brought new species into new areas but also influenced the severity of the disturbance.

The most direct effect of the advancement of outbreak ranges of mountain birch defoliators is an increased and/or prolonged defoliation pressure straining the mountain birches for 4–6 years instead of 2–3 years. In areas with a longer history of sympatric *E. autumnata* and *O. brumata* outbreaks, the population peaks successively follow each other with a 2- to 3-year lag (Tenow *et al.*, 2007): when the density of one species starts to decline, the density of the other species is increasing rapidly. A similar pattern was observed in the newly established outbreaks of *O. brumata* (Klemola *et al.*, 2008), creating a period of nearly 6 years of high defoliation pressure on mountain birches. The back-to-back population peaks resulted in vast areas of leafless trees. Furthermore, visible changes in the underground vegetation were observed in

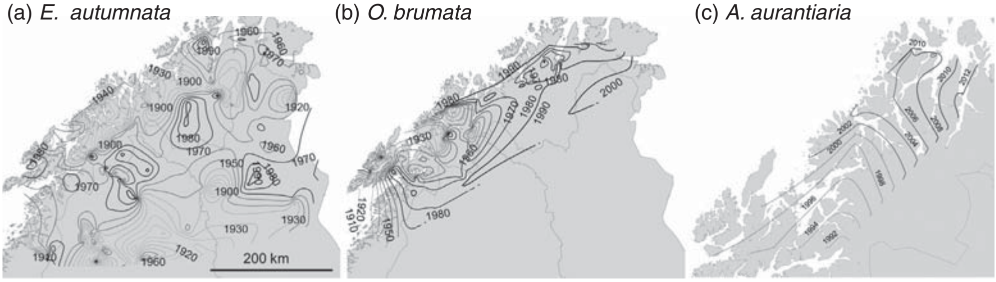

Fig. 13.4. A visualization of the year of first recorded larval outbreak for each of the three moth species in northern Fennoscandia. Contour lines were calculated from a continuous surface derived using natural neighbour interpolation between outbreak localities for: (a) *Epirrita autumnata* (*N*=312); (b) *Operophtera brumata* (*N*=116); and (c) *Agriopis aurantiaria* (*N*=21) in northern Fennoscandia. (Modified from Jepsen *et al.*, 2008. Data for *A. aurantiaria* from Jepsen *et al.*, 2011, and unpublished records (K. Ruohomäki). Note that an 'outbreak' in this context covers a wide range of larval densities.)

northern Norway, Sweden and Finland (see Section 13.3.2 and Jepsen *et al*., 2013), marking the cascading effects of geometrid outbreaks.

For now, *A. aurantiaria* is lagging in phenology to its host plant. With the warming climate in spring, the phenology match is likely to create improved conditions for the newcomer. The plausible scenario for this species is likely to result in 9- to 11-year outbreak dynamics similar to *E. autumnata* and *O. brumata* (Jepsen *et al*., 2011). In that case, the series of moth population peaks following each other may go from two to three, increasing the defoliation pressure markedly. The resulting trophic cascades after outbreaks may have further intensified consequences in the mountain birch ecosystem, which will strain the ecosystem's ability to recover.

The low number of species in this subarctic ecosystem, on the other hand, may indicate a low resistance against changing climate. Modified/altered species interactions brought about by climate change will have significant consequences for the ecosystem. The overall connectedness might not alter due to climate change, but the number of interactions between native species may be reduced due to species invasions (Ings *et al*., 2009).

The changes already noted in community composition are likely to affect species interactions. With the emergence of new, similar outbreak species, not only the interaction between the geometrids and the host plant but also those between geometrids and higher trophic levels are bound to change. The geometrids, *E. autumnata* and *O. brumata* in particular, share natural enemies (Klemola *et al*., 2009, 2014). A preference of the invertebrate and vertebrate predator guild on *O. brumata* in new sympatric outbreak areas was found in a long-term study (Klemola *et al*., 2014). These types of predator preferences have the potential to alter the population dynamics of the geometrids (Ammunét *et al*., 2014). The resulting effects on other trophic levels may have the potential to take the ecosystem over a tipping point, altering the dynamics of the system in a profound way.

13.5 Conclusions and Future Directions

Warming trends in winter and spring temperatures have aided the observed range expansions of geometrid outbreaks in northern Fennoscandia. This has created an intensified disturbance regime of spatially and temporally extended outbreaks, and caused an abrupt and severe ecosystem disturbance. We are only just beginning to unravel the short-term implications of this for the mountain birch forest ecosystem. However, the resulting long-term changes in trophic-level interactions may be enough to transfer the ecosystem over a tipping point. Current understanding of the climatic drivers of moth development, distribution and trophic interactions with the host plants and natural enemies of the geometrids is insufficient to formulate predictions of the long-term implications of continued climate change for the system. There is a need to continue the long-term monitoring of geometrid dynamics, in combination with experimental research targeted at resolving questions related to the following: (i) specific temperature regulators of moth egg hatching and birch development for a better understanding of the conditions permitting a phenological match with the host plant at larval emergence; (ii) the consequences of invading geometrids on the native trophic network, including interactions with natural enemies; (iii) the causes and consequences of lagged population peaks in sympatric moth species; (iv) the cascading effects of outbreak-induced vegetation state changes on other trophic levels, such as other herbivores; and (v) the resilience of the birch forest to recurrent outbreaks in combination with other stressors, such as grazing/browsing, moisture stress and continued warming.

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14 Effects of New Forest Management on Insect Damage Risk in a Changing Climate

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Abstract

Recent findings suggest that damage by forest insect pests will increase as a consequence of climate warming. Here, we ask whether changes in forest management can alter and possibly mitigate the increased risk of damage and outbreaks. We focus mainly on conditions in northern Europe, particularly Sweden, but conclusions should be valid for northern temperate forests. Three types of insect pests are considered; the regeneration pest, *Hylobius abietis* (pine weevil), defoliators and the bark beetle, *Ips typographus*. We compare the expected effect of new management methods with the presently predominant method of even-aged stands, which are thinned two to three times before final harvest by clear-felling. Continuous cover forestry (CCF) is the method most different from the present practice. CCF would lead to a drastic decrease in pine weevils, and also less damage by defoliators, but this latter prediction is uncertain. For the bark beetle, the uncertainty is even greater. In mixed forests, all three insect pest types are expected to become less of a problem. Putative mechanisms involve more abundant and diverse natural enemy fauna, and a more scattered distribution of food resources. A shorter rotation period (including no thinning) is expected to increase the damage by pine weevils, as it will result in more abundant breeding material. For defoliators, it is difficult to foresee the effects. A shorter rotation period will decrease the risk of bark beetle outbreaks, as storm-fellings will be less frequent and young stands more common. The effects of exotic tree species and clonal forestry are complex and will depend on several factors. A general conclusion is that forest management may be used to mitigate the anticipated risk of insect pest damage as a consequence of climate warming, but more research is required to certify these indications.

14.1 Introduction

All insect populations are, to a lesser or greater extent, affected and normally regulated by bottom-up (plant resource quality and quantity), horizontal (competition) and top-down (natural enemy impact) processes (Berryman, 1999). Nevertheless, all insect populations undergo fluctuations in density,

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but when a species occasionally reaches densities that cause damage exceeding some critical threshold that is unacceptable to humans, it is considered a pest species. Some pests, like the pine weevil (*Hylobius abietis*), are what we may call constant pests and cause damage at high levels most of the time, whereas other pests, like many bark beetles and defoliators, have more eruptive outbreaks. Eruptions are commonly triggered by specific external factors (e.g. climate) and possibly result in severe damage before populations break down again (Berryman, 1986; Wainhouse, 2005; Barbosa *et al*., 2012).

Several external factors affect the regulating processes, and thus the level of damage and risk of outbreaks (Berryman, 1999). Two important factors are climate and land use, or in this case more specifically forest management (Wainhouse, 2005). Here, we assume that climate warming generally increases the levels of damage and the risk of outbreaks (Netherer and Schopf, 2010), even though damage levels and risk of outbreaks in some cases are showing no or opposite trends, and ask to what extent changes in forest management can mitigate these unwanted anticipated consequences.

We have decided to restrict the geographical area considered and focus on northern Europe, Fennoscandia and in many cases, Sweden only. One reason for this is that it is easier to foresee potential changes in forest management at national and regional scales. However, many of our conclusions should be valid for forests in northern temperate regions.

As background information, it can be noted that the production forest area in Sweden, which covers 23.1 Mha, is dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), constituting 42% and 39% of the standing forest volume, respectively.

14.2 Types of Forest Insect Pests, Including Mechanisms of Population Dynamics

Insect pests in Fennoscandian forests can be divided into a few types that cause damage during different stages of a forest rotation period. We will focus here on three major types that are presently causing most of the damage: regeneration pests, defoliators and bark beetles. Other pest types with the potential to cause severe damage are sucking insects (e.g. aphids), shoot borers and cone insects. At present, and historically, these other pests have more local and restricted impact, but with a changing climate and alterations in forest management they might become more important.

14.2.1 Regeneration pests

Regeneration pests, particularly the pine weevil, *H. abietis*, constitute a severe threat for young seedlings. The immense problem with the pine weevil as a pest of planted seedlings in forest regenerations is related directly to management by clear-felling followed by replanting (Wainhouse, 2005; Nordlander *et al*., 2011). Current management in large parts of northern Europe with a mosaic of even-aged stands that are clear-felled when they have reached an optimal size also appears ideal for the pine weevil. This is because the size of the pine weevil population is largely determined by the amount of available breeding material, i.e. fresh conifer stump roots (Eidmann, 1977). Hence, a constantly high population level of this very mobile insect is maintained in the landscape by human’s harvesting similar amounts of forest every year.

14.2.2 Defoliators

Defoliators may attack trees during the whole rotation period. Populations of defoliators are usually regulated at modest levels by a combination of bottom-up and top-down processes, acting via their host trees and natural enemies, respectively. Several species of needle- and leaf-feeding insects occasionally appear in outbreak densities, defoliating vast forest areas, sometimes for an extended number of years. Both deciduous and conifer trees usually survive single years of defoliations, but incremental growth is reduced. If severe defoliation is repeated for several years, it can lead to tree mortality caused by resource depletion and/or secondary agents such as bark beetles, longhorn beetles and fungal diseases (e.g. Cedervind *et al*., 2003). The European pine sawfly (*Neodiprion sertifer*) and the large pine sawfly (*Diprion pini*) are the main defoliating insects in boreal pine forests in Fennoscandia. Other species that rarely reach high densities in pine stands are the pine looper moth (*Bupalus piniaria*), the pine tree lappet moth (*Dendrolimus pini*), and the pine beauty moth (*Panolis flammea*). Sporadic defoliating outbreaks in spruce and pine forests by the nun moth (*Lymantria monacha*) have also been reported. Several hardwood tree species are occasionally defoliated by Lepidoptera larvae, in oak mainly by *Operophtera* spp. and the European leaf roller (*Tortrix viridiana*). In mountain birch forests, the main factor driving the dynamics is recurring outbreaks of geometrids, mainly the autumnal moth (*Epirrita autumnata*) but also the winter moth (*Operophtera brumata*). Two species, the gypsy moth (*Lymantria dispar*) and the larch tortrix (*Zeiraphera griseana*), which are causing substantial defoliations in more southern parts of Europe, have on a few occasions been reported to defoliate forest areas in northern parts of their distribution range.

14.2.3 Bark beetles

Bark beetles are major forest pests at the later part of the rotation period, when trees have reached a certain size. The European spruce bark beetle, *Ips typographus*, kills large volumes of mature spruce forests during outbreaks, and thus is one of the most important forest pests in Europe (Grégoire and Evans, 2004). Population dynamics are driven primarily by bottom-up forces, such as the availability of susceptible host trees, while enemies seem to be of less importance (Økland and Berryman, 2004; Marini *et al*., 2013). Outbreaks are often initiated by storm and drought disturbances (Christiansen and Bakke, 1988; Wermelinger, 2004; Rouault *et al*., 2006; Marini *et al*., 2012). The surplus of weakened trees releases the beetles from the strong intraspecific competition that they generally experience, which results in a population increase. Higher attack densities increase the beetles' ability to overcome the defences of living trees, which also may be reduced in the case of drought (Komonen *et al*., 2011). Commonly, trees are killed in groups as a result of the switching of attracted beetles from fully colonized to nearby trees (Schlyter and Anderbrant, 1989). The risk of tree mortality is strongly enhanced close to large infestations from the previous year (Kautz *et al*., 2011).

Risk assessment for infestations by the spruce bark beetle is based mainly on the probability of storm damage, stand rotation period (older stands = higher risk) and growing stock of mature spruce (higher volumes = higher risk). But also other factors like tree defences, nutritional quality of the breeding substrate, tree switching and natural enemies are discussed. Even though natural enemies are not driving the population dynamics, they may cause as much as 80% reduction of reproductive success (Weslien, 1992). Thus, their densities may influence the probability of bark beetles overcoming tree defences in individual stands. Drought was not included because of a lack of information on how forest management affects the risk of drought stress of trees.

14.3 Anticipated Effects of Climate Change

All insects are expected to respond positively to the most obvious and most commonly observed climate change effect, i.e. increased temperatures. The reason is, of course, that insects are ectotherms. The positive response to increased temperatures has also been manifested in changed distribution patterns into areas previously uninhabitable due to too low temperatures. However, the effect on insect numbers, and hence damage on plants, is less straightforward, mainly because not only the insect pests but also their host trees and their natural enemies respond to the same environmental changes. The outcomes of the changes in interactions in more or less complex food webs are not easy to foresee (Berggren *et al.*, 2009).

For the sake of simplicity, we make the overall assumption that the insect pests considered here all respond positively to climate warming and that damage will increase accordingly (Fig. 14.1). Some of the reasons behind this assumption are given below.

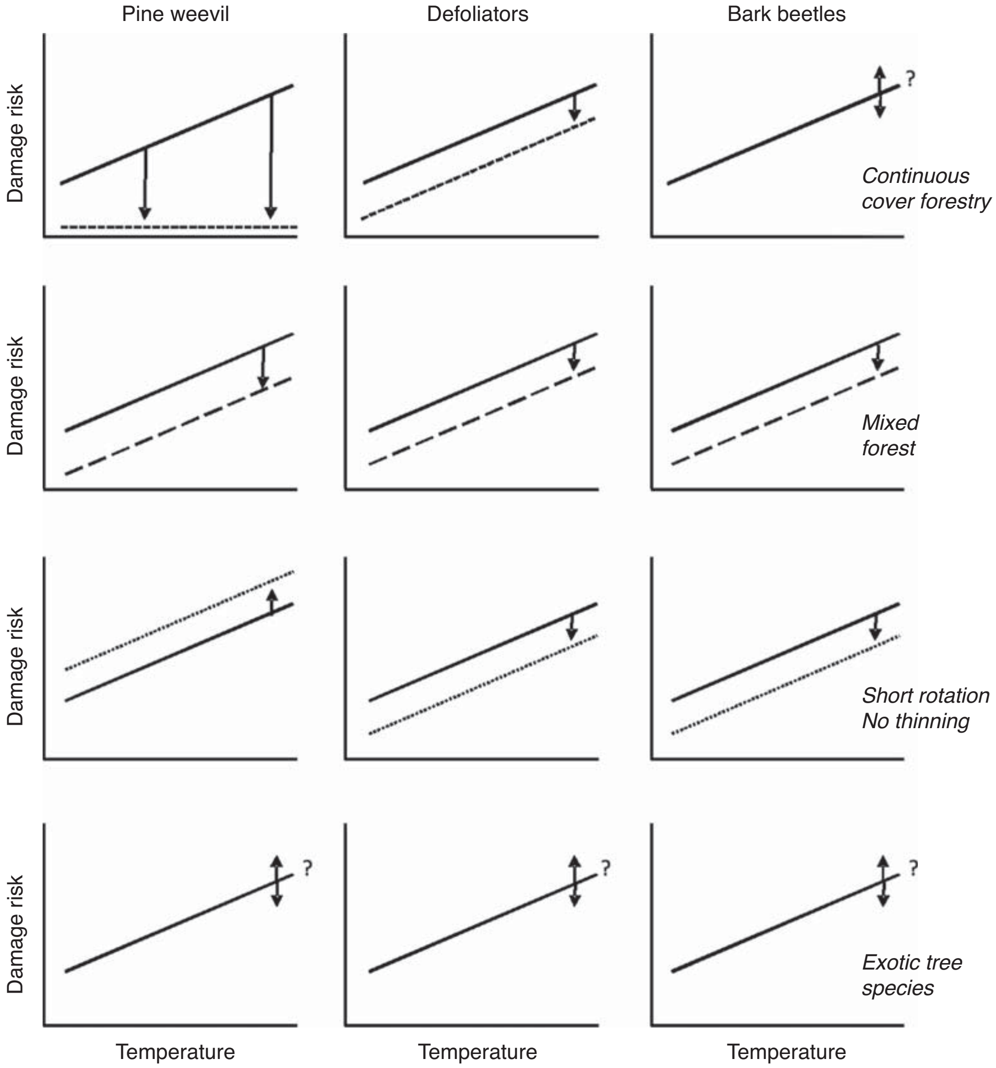

Fig. 14.1. Visualization of the expected effects on the risk of insect damage by three types of pests (a regeneration pest, defoliators and bark beetles) if forest management is changed (arrows) from the predominant practice of clear-felling of even-aged stands, after two to three thinnings, to four 'new' management methods (dashed lines): continuous cover forestry; mixed forest; short rotation including no thinning; and exotic tree species. The basic scenario (solid line) is an anticipated increased risk of damage with increasing temperature, *sensu* climate warming.

14.3.1 Regeneration pests

A warmer climate in northern Europe is expected to increase the risk of damage to conifer seedlings by the pine weevil (Inward *et al.*, 2012). A shorter generation time (which varies from 1 to 4 years) may contribute to this, although probably more important will be that the number of days during the year with temperatures suitable for weevil feeding increases. In large parts of Europe north of the Mediterranean region, a warmer climate would certainly lead to a longer activity period for the pine weevils in both spring and autumn. In summer, the weevils are mainly active during night and morning hours (Fedderwitz *et al.*, 2014), so heat is probably limiting feeding mainly under clear periods with hot days and cool nights (Christiansen and Bakke, 1971). Thus, a main effect of a warmer climate would be prolonged periods of feeding of the pine weevil, and probably also more damage. Another possible reason for increased damage is that a higher proportion of pre-reproductive weevils will have a period of feeding in the autumn before hibernation, instead of just remaining in the pupal chamber for hibernation. However, exactly how temperature conditions affect the 'choice' between these alternatives remains to be investigated (Wainhouse *et al.*, 2014).

14.3.2 Defoliators

It has been discussed widely as to whether or not a warming climate will increase the damage level to trees by and the risk of outbreaks of defoliators. A warming climate is expected to affect both directly and indirectly the performance and population dynamics of forest defoliators, but the resulting outcome is hard to predict and is dependent on several factors, not least how the abundance and efficiency of natural enemies and food quality and quantity are affected (e.g. Berggren *et al.*, 2009; Kollberg *et al.*, 2013). Warming combined with likely changes in precipitation will also affect the performance of defoliators, and hence the damage levels (Jactél *et al.*, 2012). The most common forest defoliating outbreak species in Europe have univoltine life cycles, which are not expected to change in the near future. However, it is expected that both their distribution and outbreak range will change in a warming climate (Vanhanen *et al.*, 2007), which has already been documented for some geometrid moths and the pine processionary moth (e.g. Battisti *et al.*, 2005; Jepsen *et al.*, 2008). Klapwijk *et al.* (2013) have analysed the estimated changes in area of defoliated forest in Hungary by six forest Lepidopteran defoliators over the past five decades. During these 50 years, the annual mean temperature in Hungary increased by 1.5°C, while annual precipitation did not change. The trend in area defoliated by two species increased, defoliation by three species showed no trend, while the area defoliated by one species possibly declined. A study of the changes in damage severity indices and the outbreak dynamics of five pine-defoliating species in southern Germany over >200 years (Haynes *et al.*, 2014) also shows individualistic responses to variation in temperature and precipitation. In two species, outbreak cycles ceased in relation to warming temperatures, and two species showed higher outbreak frequencies. The latter change may also be attributed to recent changes in forestry practices coinciding with warming temperatures.

14.3.3 Bark beetles

The spruce bark beetle is expected to respond strongly to climate change (see Chapter 11, this volume) due to the direct effect of temperature on development time (Wermelinger and Seifert, 1998) and number of generations (Baier *et al.*, 2007; Jönsson *et al.*, 2011). An increased temperature may also affect population dynamics indirectly through drought events (Marini *et al.*, 2012, 2013) and a lower probability of frozen soil during winter, which increases storm damage. It is, however, unclear to what extent the severity and frequency of storms will change in the future. Also, tree defences, tree suitability and natural enemies may be affected by climate change.

14.4 New Forest Management Methods

Forest management will most likely change to adapt to a warming climate and changed demands from the market and society. This will probably lead to the implementation of new methods and strategies affecting rotation time, harvesting systems and the use of new tree species and genotypes. Here, we describe four different forest management regimes that are all likely to become more common in the future. In Scandinavian countries mainly, the existing monocultures of even-aged Norway spruce would be replaced by new methods. The present rotation period with clear-felling in these Norway spruce stands that are thinned two to three times varies between 70 and 90 years in Sweden today, depending on local growth conditions. Standing volume at the time of clear-felling depends on site fertility and the previous thinning programme. On poor sites and/or if the stand has been thinned frequently, standing volume may be as low as 200 m^3/ha, whereas standing volume may exceed 500–600 m^3/ha on fertile sites (Ekö, 1985).

14.4.1 Continuous cover/multilayered/selective cutting

Continuous cover forests (CCFs) in Sweden will be dominated by Norway spruce and by beech in southernmost Sweden. The reason why other tree species will only make up a minor part of forest stands in CCFs is because of legal restrictions and problems with regeneration under a canopy (Lundqvist, 1989; Nilsson *et al*., 2002). Therefore, CCFs will, in most parts of the country, lead to monocultures of Norway spruce, but with a more diverse size distribution of trees than is common in today's even-aged forests.

Total standing volume in CCFs will vary between 100 and 300 m^3/ha, depending on site fertility and time since last cutting (Chrimes, 2004). On fertile sites, a higher volume can be retained after cutting. Standing volume is also affected by the time between cuttings. With short time intervals between cuttings, standing volume after cutting can be higher than if longer time intervals are practised.

Even if the major part of the stems in CCF have a relatively low diameter, the volume is concentrated to fairly large trees. In a typical CCF, about 30–50% of the volume will be in stems with a diameter above 15 cm.

The risk of storm-felling in CCFs has been debated. Less risk of storm-felling is related to the assumption that the largest trees have adapted to the wind climate and will therefore withstand higher wind-speed before they fall (Persson, 1975; Indermüle *et al*., 2005). On the other hand, CCFs may result in a higher risk of storm-felling than clear-cut forestry, because the forests are thinned every 10–25 years (it is well known that thinning increases dramatically the risk of storm-felling) and it is the dominant trees that are cut (Persson, 1975; Valinger and Fridman, 2011; Albrecht *et al*., 2012). In addition, if continuous cover forestry is practised over large continuous areas, there will be fewer newly exposed stand edges compared with clear-cut forestry, which should again reduce the risk of storm damage. Yet, the selective cuttings in CCF stands and thinnings in clear-cut forestry are more important factors to be considered in this respect because they cover much larger areas. The consequences of a storm-felling are more severe in CCF than in clear-cut forestry because it is much more complicated, time-consuming and expensive to create a new CCF stand than it is to create an even-aged stand (Drössler *et al*., 2014).

14.4.2 Mixed forest

Forests can be a mix of almost all available tree species in many different proportions. This text will concentrate on mixtures of Norway spruce and birch, since it is one of the most common tree species compositions in Sweden. Stand treatments in mixtures are currently not very different from stand treatments in monocultures. Thus, mixed stands are thinned two to three times and the volume before final felling is about 300–600 m^3/ha, depending on fertility and rotation length.

The proportion of birch in the mixture is typically high in young stands and decreases with stand age (Fahlvik, 2005). In order to keep a certain proportion of birch until the end of the rotation period, heavy thinnings of Norway spruce, a strong competitor for birch, are often needed.

As for CCFs, there are contradicting opinions about the risk of storm damage in mixed stands. Some studies claim that the risk of storm damage is reduced in mixed stands because Norway spruce in mixtures is more adapted to high wind speeds than similar-sized trees in monocultures (Schutz *et al*., 2006; Valinger and Fridman, 2011; Albrecht *et al*., 2012). However, cases where mixed forests have been storm-felled to a higher degree than monocultures have also been reported, and the explanation for this could be that the 'gaps' defoliated birches constitute result in turbulent wind (Nørgaard Nielsen and Larsen, 2001).

The risk of drought in mixed stands compared to monocultures is rarely studied. There exists a not yet empirically well-studied hypothesis that mixtures could be an advantage because trees of different tree species exploit different soil layers (Man and Lieffers, 1999). One of the few empirical studies indicates that Norway spruce in mixture with European beech suffers more drought stress than in pure spruce stands (Schume *et al*., 2004).

14.4.3 Shorter or longer rotation period (including no thinning)

In the following, we will mainly describe the effects of shorter rotations without thinning in Norway spruce stands as compared to the currently normal stand treatment programme with two to three thinnings and final felling at an age of about 70–90 years. Longer rotation periods, used to support endangered species and biodiversity, are normally restricted to relatively small areas. The impact of these areas may be important at local scales but are probably negligible in most cases on regional scales.

The rotation length in short-rotation forestry is dependent on the development of mean annual increment (MAI). For Norway spruce, MAI increases relatively rapidly up to a certain point, where it reaches a plateau. When MAI has reached about 90% of its maximum; it stays at this level for at least 30 years, but in many cases even longer (Pretzsch, 2009). Clear-felling the forest is therefore possible within a wide range of harvesting ages without losing more than about 10% of potential production. However, if clear-felling is done before MAI has reached 90% of its maximum value, a large proportion of the potential production may be lost, and this is in most cases uneconomical. Depending on fertility, the shortest possible rotation without substantial loss of production varies between 35 and 60 years. However, the rotation length can be shortened even more on low productive sites by the use of intensive fertilization (Bergh *et al*., 2008). Short rotations normally do not include thinnings, which would prolong rotation lengths.

Reduced risk of windthrow is one of the strongest incentives for the introduction of shorter rotation periods. The probability of windthrow is increased significantly during a 5- to 10-year period after thinning, and generally increases with the height of the trees (Persson, 1975). In short-rotation Norway spruce stands, thinnings are avoided and trees are cut at a lower age and height compared to current practice (Persson, 1975).

There are also, however, a number of disadvantages associated with short-rotation forestry. One major drawback is that it is very inflexible. The time for clear-felling can only be varied within a limited time frame if the path of short rotation without thinning has been chosen. Because the stands are unthinned, self-thinning will be substantial, with big losses of volume if the stands are kept longer than about 10–15 years after the first possible time for clear-felling (Elfving, 2010). Another disadvantage is that the forest owner has to wait for a long time for the first net income, especially when calculating for individual stands. Economic limits decrease with estate size, when age structure is more diverse and different stands can be cut almost every year.

Shortened rotation of Norway spruce stands is very uncommon in Sweden. Damaging agents that have not yet been experienced might occur in these dense, unthinned stands. Furthermore, in case of disturbance, salvage cutting will be more difficult since there are no strip-roads to extract harvested trees.

14.4.4 Exotic tree species and clonal forestry

In this chapter, we will go only briefly through the use of new tree material in forestry. The reason is that there are many available options and there are no clear trends. New tree material may involve the introduction of non-native, exotic tree species and new tree genotypes. Depending on which tree species or genotypes are selected, and how they are mixed at local and landscape scale, will affect how insect pests respond.

The exotic tree species most commonly discussed for introducing in Sweden are Douglas fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), sycamore maple (*Acer pseudoplatanus*), hybrid aspen (*Populus tremula tremuloides*) and hybrid larch (*Larix eurolepis/Larix marschlinsii*). All of these species presently occur on minute areas. Lodgepole pine (*Pinus contorta*) is an exception as it now grows on about 600,000 ha in northern Sweden. The uncertainty about the ecological risks – including pests – of introducing exotic tree species on a larger scale is considerable (Felton *et al*., 2013).

Clonal forestry involves breeding for high productivity and improved wood quality. Resistance against insect pests is seldom a priority. Therefore, it is a risk that more clonal forests may increase the risk of insect damage and outbreaks. However, this risk may be counteracted by the practice to plant multiple genotypes in the same stand.

14.5 Effects of New Forest Management Methods on Insect Pests

14.5.1 Continuous cover/multilayered/selective cutting

Regeneration pests

A transition from the management of even-aged conifer forests by clear-felling followed by planting to multilayered CCF stands would certainly lead to a drastic decrease in damage caused by the pine weevil. This has already been seen in Germany (Långström and Day, 2004), where even-aged management has largely been abandoned in favour of a transformation to CCF stands during the past two to three decades (Kenk and Guehne, 2001). The damage decline can be attributed both to a lower reproduction rate of the pine weevil in multilayered forests and to the fact that naturally regenerated seedlings suffer less damage than planted seedlings.

Management of CCF stands means the cutting of single trees or small groups of trees. The fresh stump roots, which constitute the breeding substrate of the pine weevil, therefore become more or less shaded, which tends to result in a longer development time for the immature stages compared to a development in sun-exposed stumps on a clear-fell site (Bakke and Lekander, 1965; Inward *et al*., 2012). Moreover, since the pine weevils migrate by long-distance flight high above the tree canopies in their search for sites with breeding material (Solbreck, 1980), scattered stumps within forest stands should be less likely to be located by the weevils than stumps aggregated on clear-felled areas. These factors point to a lower reproduction rate and lower population density in landscapes dominated by CCF stands.

Because CCF stands are usually renewed by natural regeneration, the risk of damage to seedlings by the pine weevil is far less than for planted seedlings on clear-cuts. The less severe damage to naturally regenerated seedlings (Selander *et al.*, 1990) is probably because it takes time for the nursery-raised seedlings to establish and achieve the full effect of their resin defence system (Wallertz and Petersson, 2011). To summarize, a massive transfer from even-aged to multi-layered CCF stands over large geographical areas should largely reduce the economically important damage by the pine weevil.

Defoliators

Forests with a diverse size and age structure as CCF stands are believed to be less prone to suffer from severe defoliations. One reason could be that there is a lower probability that most trees in a stand are of the same quality as food for the defoliators in a CCF stand than in an even-aged stand, since food quality for insect herbivores can be related to tree age (e.g. Donaldson *et al.*, 2006). Speculating, a similar argument could be made for natural enemies; it is more likely that the pressure from natural enemies is similar among trees in an even-aged stand than if trees are of different ages and vary in physical structure, microclimate and light conditions, affecting the number of suitable hosts, complementary food sources and shelter structures, which in turn has implications for the structure of the invertebrate community (Jefries *et al.*, 2006). However, knowledge of the effects of CCFs on defoliators is meagre, but a recent study on pine defoliator outbreak dynamics in southern Germany, where forestry practices have changed towards CCFs, point out that recent changes in the dynamics of some species could be a combined effect of climate change and changed forest management (Haynes *et al.*, 2014).

Bark beetles

No empirical studies have compared the damage caused by the spruce bark beetle in CCF and even-aged stands. A modelling study predicted higher tree mortality in CCF stands (Seidl *et al.*, 2008). However, the damage level per volume unit of growing stock was not calculated (the growing stock was higher in the uneven-aged stand) and the modelling included the transition period from more even-aged to uneven-aged conditions. As mentioned above, it is not clear if the risk of storm damage is different in CCF stands compared with the baseline alternative. The probability of the local beetle population reaching the threshold for overcoming tree defences will be lower in uneven-aged stands as a result of the lower growing stock of spruce (i.e. lower volumes of storm-felled trees in the case of storm damage and of standing attacked trees per hectare). On the other hand, there will always be mature trees available in CCF stands. The greater spacing between mature trees should reduce the risk of successful switching from colonized standing trees to nearby living trees. CCF stands include trees with both higher (dominant trees) and lower (suppressed trees) nutritional quality as breeding substrate. The ratio of enemies per spruce bark beetle may be higher because of the continuous presence of small diameter trees more suitable for other bark beetle species than the spruce bark beetle. Altogether, because of uncertainty of the storm resistance of CCF stands, it is hard to conclude if damage risk is greater or lesser compared with the baseline alternative. However, if a transition period (when converting mature even-aged stands to CCF stands) is also included in the assessment, the risk should increase strongly as a result of repeated thinning in mature spruce stands.

14.5.2 Mixed forest

Regeneration pests

Planted conifer seedlings should suffer less damage by the pine weevil in regenerations resulting from the harvest of a mixed spruce/birch forest compared to an ordinary even-aged spruce stand. Because pine weevils use conifer stump roots as breeding substrate, they migrate *en masse* by flight to areas with freshly cut conifer trees (Solbreck, 1980). Host volatiles from the conifer stumps aid the pine weevils in their orientation to suitable breeding sites (Nordlander *et al*., 1986). A harvested mixed forest contains fewer spruce stumps emitting attractive volatiles than a pure spruce stand, and in addition, the stumps of deciduous trees emit volatiles that might reduce the attraction of pine weevils, as has been shown for several bark beetles with conifer hosts (Zhang and Schlyter, 2004; Danielsson *et al*., 2008). Thus, the number of immigrant pine weevils should decrease with the increasing proportion of deciduous trees in the harvested stand, and this should result in less damage on seedlings planted in the area.

On a wider geographical scale, pine weevil population density should be lower in a landscape dominated by mixed forest as compared with conifer forest. The pine weevil population level is determined primarily by the amount of available breeding substrate (Eidmann, 1977), i.e. fresh conifer stump roots (or roots of trees killed by storm or fire). This resource is reduced with an increasing proportion of deciduous trees, and consequently the pine weevil population, and thereby also damage, should generally decrease.

Defoliators

It is generally suggested that the risk of herbivore damage is lower in mixed stands compared to a monoculture. However, the risk also seems to depend on the composition of tree species, which insect herbivore species are present and how specialized they are (Jactél and Brockerhoff, 2007; Vehviläinen *et al*., 2007, 2008). Further, the risk may be related to the growth condition of the trees, which in turn may influence the resistance capacity of the trees to insect herbivory (drought stress; Pretzsch *et al*., 2013). Also, the consequences of an outbreak in a mixed stand may differ for different tree species compositions, and successional growth may have a different ratio of tree species when the forest grows back.

It has been indicated that herbivory by more specialized insect herbivores is reduced in stands with a higher tree species diversity or ratio of non-host tree species (e.g. Castagneyrol *et al*., 2014). The lower number of suitable host trees in relation to dispersal ability as well as higher diversity and abundance of insect predators are factors suggested to influence the risk of outbreaks. For example, the survival of European pine sawfly larvae (*N. sertifer*) was lower on pine trees in mixed birch and pine stands compared to pure pine stands associated with a higher abundance of ants (Kaitaniemi *et al*., 2007). However, at the same time, the abundance of ant-tended aphids was higher in the mixed stands, so the net effect for the long-term performance of pines was hard to predict.

In mixed stands, the defoliation risk by polyphagous insect herbivores is partly dependent on tree species composition and species suitability. Polyphagous insect herbivores are rarely exerting a high herbivore pressure, but if conditions are favourable and the current trees are within the host range, the outbreak risk increases. The abundance of the polyphagous nun moth (*L. monacha*) and the beech specialist pale tussock moth (*Callitera pudibunda*) was investigated by using light traps in a gradient mixture from pure beech stands to pure spruce forests in Germany. As expected, specialist pale tussock moth abundance increased dramatically in the pure beech stands, while the nun moth trap catches varied along the gradient and were low and least variable in the pure beech stand (Heiermann and Schütz, 2008). Pine growth reduction in mixed pine–oak stands following an outbreak by the pine sawfly (*D. pini*) was almost 100%, while the oak trees suffered little damage and increased their growth for several years following the sawfly outbreak (Perot *et al*., 2013).

In a spruce–birch stand, the consequences of defoliation are most severe if the spruce trees are attacked. That may lead to a high incidence of tree mortality, either directly or from secondary agents (insects or pathogens). Deciduous trees have a higher capacity and are better equipped to recover and withstand defoliation, even though incremental growth will be reduced temporarily. However, conifer trees also have different sensitivity to defoliation. In a mixed stand of balsam fir and black spruce, the extent of tree mortality was directly related to the proportion of the less sensitive black spruce in the stand. It has therefore been recommended to increase the proportion of black spruce in mixed stands, to reduce overall tree mortality caused by outbreaks of the spruce budworm (Pothier *et al*., 2012).

Bark beetles

Spruce bark beetle damage should be lower in mixed stands compared with that in pure spruce stands. Empirical studies show a positive non-linear relationship between the percentage of spruce and the risk of spruce bark beetle damage (Netherer and Nopp-Mayr, 2005; Overbeck and Schmidt, 2012). Also, a modelling study predicted less damage compared with pure spruce stands, but the damage level per volume unit of growing stock was not reported (Seidl *et al*., 2008). It is not clear how the risk of storm damage in mixed stands compares with the baseline alternative (see above). The probability of the local beetle population reaching the threshold to overcome tree defences will be lower in mixed stands as a result of the lower growing stock of spruce (i.e. lower volumes of storm-felled trees and of standing attacked trees per hectare). The probability of colonization of wind-felled and standing trees may be lower as a result of non-host volatiles released from birch interfering with pheromone communication (Zhang and Schlyter, 2004). In addition, the probability of switching to nearby trees will decrease as a result of larger spacing between spruces.

14.5.3 Shorter or longer rotation period (including no thinning)

Regeneration pests

A more intensive forestry with a shorter rotation period would probably lead to further raised population levels of the pine weevil and increased damage. The basis for this prediction is that intensified forest management leads to an increased volume at harvest due to no thinnings, and thereby also more stump roots on clear-fell sites available as breeding material. However, it is not known exactly how pine weevil reproduction is related to stump density and size, i.e what stump density results in a maximum amount of root bark suitable for larval development.

Management of conifer forests with a relatively short rotation period usually entails no thinning. Stumps created by thinning may provide breeding material for the pine weevil, but the number of larvae developing in stump roots within forest stands has been reported to be relatively low (Korczynski *et al*., 2007). Little is known, however, regarding the extent to which stumps from thinnings contribute to the total amount of breeding material utilized by the pine weevil.

For biodiversity and conservation purposes, a longer rotation period than that used in normal production forests can be employed. With similar reasoning to above, this should result in less breeding material for the pine weevil. In reality, however, this effect may be negligible, because the stands with a prolonged rotation period will probably constitute a quite limited fraction of the forest landscape; and as always, when evaluating effects on the pine weevil population, a vast geographical area must be considered.

Defoliators

Changes in rotation period can be expected to affect the impact of insect defoliators on forests in two ways. First, some insect species are prone to reach high densities on trees of a certain age class: an analysis of forest tent caterpillar defoliation of aspen trees in Canada in 1999–2006 showed that 50-year-old trees were most likely to be defoliated, while younger and older stands suffered less damage (Charbonneau *et al*., 2012). Second, although most herbivorous forest insects are not that dependent on stand age, defoliation from severe outbreaks may still have a different impact on growth in stands of different age: in stands defoliated by the pine processionary moth, stem incremental growth was reduced most in older trees (Jaquét *et al*., 2013). The likelihood of defoliator densities reaching high levels is, however, probably related more to stand characteristics and stand condition than to stand age.

Stand age has been considered as one of the important factors when predicting even-aged forest stands' susceptibility to forest defoliators in both deciduous and conifer tree species. It has also been suggested that young trees could be better protected from insect herbivores by higher levels of secondary plant compounds than old trees (e.g. Donaldson *et al*., 2006). In an outbreak of the large pine sawfly (*D. pini*) in Finland, the intensity of defoliation was, as expected for this species, highest in mature stands and on larger trees, but younger stands were also quite commonly subjected to high levels of defoliation (De Somviele *et al*., 2004). This, and other studies, suggests that factors at both a local and a landscape scale affect the susceptibility and dynamics of defoliation when an outbreak has started, which calls for including multiple scales in efforts to reveal the mechanisms behind defoliator outbreaks (Charbonneau *et al*., 2012). Structural factors at different scales may be related to the dynamics by affecting, for example, the dispersal ability of the defoliator (Foster *et al*., 2013) or temperature variability and the presence of natural enemies (Soubeyrand *et al*., 2009).

Although some studies have shown that defoliation levels and insect pest densities are lower in unmanaged compared to managed pine stands (e.g. Veteli *et al*., 2006), and thinning has been suggested as a method to intervene in ongoing outbreaks of defoliators, there is no clear picture of the effects, and results are usually based on correlative relationships (Liebhold, 2012). However, a recent North American experimental study suggests that thinning may increase tree and stand resistance in different conifer species to low levels of spruce budworm defoliation for several years (Bauce and Fuentealba, 2013). The effect differed in strength and duration between tree species, thinning intensity, site drainage and year after treatment. The reduced damage was due mainly to increased tolerance by an increased amount of foliage and less an effect of chemical defence substances reducing defoliator performance. Also, other studies indicate that thinning initially seems to affect the amount of foliage and nutritional value of the trees, which benefits the defoliators compared with denser control stands, but that in turn leads to an increased tolerance to herbivory in thinned stands (Moreau and Quiring, 2011). Further, the total growth loss was lower in thinned oak stands compared to denser stands that had experienced equal levels of defoliation by the gypsy moth (*L. dispar*), due to better growth (recovery) the years following the defoliation (Fajvan and Gottschalk, 2012). Thus, discarding thinning could be expected to result in more or less damage to trees depending on how insect densities change in relation to the amount of foliage available.

Bark beetles

A shorter rotation period will decrease, while a longer will increase, spruce bark beetle damage compared with the baseline alternative. Empirical studies show that the risk of formation of infestation spots increases with a growing stock of spruce (Kärvemo *et al*., 2014; Pasztor *et al*., 2014) and a positive, non-linear relationship between stand age and the level of spruce bark beetle damage (Netherer and Nopp-Mayr, 2005; Overbeck and Schmidt, 2012). A prolonged rotation period means a higher risk of storm damage as a result of a larger part of the rotation period with mature trees, thinnings and higher tree heights, while the opposite is true for a shortened rotation period (Valinger and Fridman, 2011; Albrecht *et al*., 2012).

14.5.4 Exotic tree species and clonal forestry

Regeneration pests

The use of non-native conifer species may result in either decreased or increased damage by the pine weevil, depending on the tree species. The severity of the damage will depend on how attractive the seedling bark is to adult pine weevils and the seedling's defence to and tolerance of feeding damage (Carillo-Gavilán *et al*., 2011; Zas *et al*., 2011). With extensive use of introduced species, their suitability as hosts for larval development may also affect the pine weevil population level, and thereby damage risk (Thorpe and Day, 2002).

The pine weevil is native in large parts of Europe and Asia where conifer forests occur. Many conifer species of different genera are used, both for larval development and as food for the adult weevils; species of *Pinus* and *Picea* seem to be preferred but *Abies* and *Larix* are also used as hosts (Thorpe and Day, 2002; Olenici and Olenici, 2007; Wallertz *et al*., 2014).

The large-scale use of introduced conifer species in northern Europe mainly includes species from North America, i.e. outside the natural range of the pine weevil. In addition, some introductions have been made of *Larix* and *Abies* species originating from within the natural range of the pine weevil. Recent studies have shown that two of the North American species, Douglas fir and Sitka spruce, are maybe even more attractive as food for adult pine weevils than the main native host species, Scots pine and Norway spruce (Wallertz and Malmqvist, 2013; Wallertz *et al*., 2014). Larval survival has also been reported to be high in Douglas fir (Wainhouse *et al*., 2001). Thus, it is possible that an extended use of Douglas fir and Sitka spruce in northern Europe could lead to even higher damage levels than in regenerations with Norway spruce or Scots pine.

Another aspect of intensified forestry is the use of genetically improved material, by ordinary plant breeding or by producing clonal material by somatic embryogenesis (von Arnold *et al*., 2005). It is not known whether such plant materials may be more or less susceptible to feeding damage compared to standard seedlings. Improved plant material is, however, more costly and more profitable to protect from damage. If plants improved for high production die young, they will be replaced by naturally regenerated trees in the final stand, and thereby the yield at harvest will be reduced. Thus, intensified efforts are needed to protect improved plant material from pine weevil damage.

Defoliators

Recently introduced tree species may escape herbivores initially or be suitable for already present insect herbivores and pathogens. It has been suggested that the taxonomic affinity between the introduced tree species and the native flora determines the likelihood for native species, especially specialist insect herbivores, to establish also on the new species. When lodgepole pine was introduced in Sweden, the species was colonized rapidly by the specialized insects feeding on the closely related Scots pine, whereas the insects colonizing lodgepole pine when introduced in England came mainly from moorland shrubs (Dalin and Björkman, 2006).

The scenario was somewhat different when white pine (*Pinus radiata*) was introduced in areas in Spain where the closely related maritime pine (*Pinus pinaster*) was native. The abundance of phytophagous insects was higher on the native maritime pine compared to the introduced white pine. This was due mainly to a higher preference of stem borers, while insects feeding in the canopy were distributed more evenly (Lombardero *et al*., 2012).

The exotic tree species that have been suggested to replace some of the spruce plantations in southern Sweden are all fairly new to Sweden but have already been grown to some extent in smaller-scale plantations. The risk of native insect pests attacking these species was judged as low to moderate, and the insect-feeding guilds considered a potential threat were, to a less extent, defoliators but mainly wood boring and sap feeding (Felton *et al*., 2013). However, there are considerable uncertainties in making predictions of the risks of pest insect attacks on these new species of host trees since both native polyphagous insect pests and new insect species that will probably occur may establish on these new tree species if plantations become more extensive and common features in the landscape. Other and more prominent threats may be pathogens and the tree species' potential for invasiveness, hybridization and influence on the local ecosystem (Felton *et al*., 2013).

Bark beetles

The spruce bark beetle has been reported to infest non-indigenous spruce species only occasionally, while other genera like *Larix*, *Pseudotsuga*, *Pinus* and *Abies* are rarely attacked (Schwenke, 1974). In a study of six North American spruce species, the reproductive success of the spruce bark beetle in pheromone-baited stem sections was of the same magnitude as for Norway spruce, while the weight of the offspring was somewhat lower (Økland *et al*., 2011). It is still unclear to what extent such trees would be colonized in the absence of pheromone baits. Regarding tree species from other genera, there is no information in the literature about reproductive success, but it could be assumed to be much lower compared with the native host species as a result of different chemical and physical properties. As plantations of non-indigenous tree species normally cover a minor part of the forest land, an adaptation of the spruce bark beetle is unlikely. To conclude, stands of exotic tree species should be less damaged than Norway spruce stands.

14.6 Conclusions and Future Research

The present review reveals large gaps when it comes to our knowledge of how different forest management methods might affect the risk of insect pest damage. Nevertheless, the general pattern is that changes in forest management will affect the risk of insect damage and outbreaks. Changing from the current prevalent practice of clear-felling of even-aged stands after two to three thinnings to any of the new management methods considered here (continuous cover forestry, mixed forests, shorter rotation period including no thinning, and exotic tree species and clonal forestry) is, in most cases, expected to reduce insect damage. This means that it would be possible to mitigate the anticipated effects of climate warming on forest insect pests. However, predictions about directions and magnitudes are uncertain. To make more accurate predictions concerning the response of insect pests to changes in management, not least in combination with changes in the climate, calls for more research. Cleverly designed field experiments and modelling efforts where researchers in forest entomology and silviculture collaborate would be a productive route forward. One promising approach for revealing how different management strategies affect the risk of damage by insect pests is to combine data from experiments and observations at different spatial scales (Liebhold, 2012). Continued work on how mixed forests might contribute to pest control via increased predation pressure would be most interesting, especially if efforts were made to quantify the control of pest species simultaneously with estimates of the effects on biodiversity. Another line of research that would be important to pursue is to study how the surrounding landscape is affecting processing operating at stand level. For example, estimating how differently managed forests, including nature reserves, in the surrounding landscape may function as sources and sinks of pests and natural enemies. The need for improved knowledge is urgent in a warming climate since species, including pests and their natural enemies, are changing their distribution range and new species of insect herbivores and host trees are constantly being introduced, not least via intensified trading.

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