phylo—genetic ecology

A History, Critique & Remodeling

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NATHAN G. SWENSON

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Contents

To Hayden Thor

Preface

Prior to graduate school, I was trained as a tropical tree ecologist. During my master's degree, I worked in a lab that studied cricket sex and speciation. Given this history, it almost seems logical that I ended up studying the phylogenetic structure of tropical tree communities both during my PhD and since. I was, and still am, fascinated by how the long history of lineages impacts the present-day structure and dynamics of communities. Uncovering these connections has always been a goal of mine in phylogenetic ecology. However, my phylogenetic ecology research and that of others has often veered away from this important goal. Our tangents have been well intentioned, but they have often used phylogenetic information in a way that is weak at best, or inadvertently misleading at worst. This has delayed a true synthesis of evolutionary history and community ecology and threatens the future of phylogenetic approaches to ecological problems.

This book was framed as an attempt to outline the field of phylogenetic ecology and, more so, to discuss where phylogenetic information can be utilized most effectively in ecology. Phylogenies are powerful pieces of data that can still make a major impact in ecology on topics ranging from conservation to community assembly. Here, I have tried to provide a pathway toward a more robust and interesting phylogenetic ecology. I expect that many readers will not agree with the remedies and critiques I have posed in this book, but I thank them for their consideration of my viewpoint. I expect that many experts in the field will be disappointed that I didn't cover their work in more detail or at all. I apologize in advance for this. It is not meant as a commentary on the importance of their work.

I have several people to thank for making this book possible. First, I would like to thank those at the University of Chicago Press who have helped and

encouraged the project over several years. I would like to especially thank Christopher Chung and Christie Henry for showing interest in the proposed book and for organizing initial reviews of the ideas and concept. I would also like to thank Scott Gast for guiding me through the peer reviews and revisions and getting me to the finish line. Everyone has been very patient and positive through the years, and it is very much appreciated.

Second, I am thankful for having a dynamic group of scientists in my lab group who have expanded the way I have thought about phylogenetic ecology, and ecology more generally, over the past decade. Specifically, I would like to thank Damani Eubanks, Yoshiko Iida, Shan Kothari, Jeff Lake, Lingfeng Mao, Boris Ngouajio, Krittika Petprakob, Vanessa Rubio, Uzay Sezen, Kiri Staiger, Natalia Umaña, Samantha Worthy, and Jenny Zambrano for keeping me on my toes and focused.

Third, I would like to thank the Smithsonian's ForestGeo Research Network (formerly the Center for Tropical Forest Science) for support and collaboration. I am particularly indebted to Stuart Davies for his encouragement, his questioning of my research, and his friendship. I would also like to thank David Kenfack and Sean McMahon, both of ForestGeo, for their interest in pursuing research projects together. I have also benefited tremendously from working with the many research affiliates of ForestGeo, including Liza Comita, Rick Condit, Alvaro Duque, Dave Erickson, Bob Howe, Dan Johnson, Andy Jones, John Kress, Jonathan Myers, I-Fang Sun, Jens-Christian Svenning, Jill Thompson, Renato Valencia, Amy Wolf, Joe Wright, and Jess Zimmerman. I would also like to thank my Chinese collaborators in the CForBio forest plot network for helping form a large number of successful collaborative adventures. I would specifically like to thank Keping Ma, Min Cao, and Zhanqing Hao for fostering early collaborative opportunities and meetings. For nearly ten years, I have had the good fortune of working closely with Luxiang Lin, Xiaojuan Liu, Xiangcheng Mi, Xugao Wang, and Jie Yang on phylogenetic ecology, and I am very grateful for their collaboration. I would also like to thank those who have visited my lab for collaboration in the realm of phylogenetic ecology: Guilherme Dubal dos Santos Seger, Juyu Lian, Jesus Lopez-Angulo, Oliver Purschke, Junjie Wu, and Caicai Zhang. I thank you all, and I have been privileged to be your collaborator.

Next, I would like to thank those who have provided generous funding for my research over the past 15 years. I thank the US National Science Foundation (NSF). The NSF Division of Environmental Biology, Division of Emerging Frontiers, and Division of Biological Infrastructure have all funded my work on phylogenetic ecology. Funding from the NSF Dimensions of Biodiversity program and the US-China subprogram, in particular, has greatly

enhanced and advanced my research program. A fellowship from the John Simon Guggenheim Memorial Foundation allowed me to pursue new angles in my functional phylogenomic and phylofloristics research interests. The Smithsonian's ForestGeo network provided early funding for me to explore the phylogenetic and functional diversity of the Luquillo Forest Dynamics Plot in Puerto Rico. The University of Maryland and Michigan State University have also served as supportive institutions for my research program. I thank you all for the support.

Finally, I thank Liwei, Eowyn, and Hayden for making me laugh and distracting me from work. This book took longer than expected because of you, and I'm glad it worked out that way.

1

Introduction and a Brief Phylogenetics Primer

The fields of ecology, evolution, and biogeography were neatly intertwined over a century ago. However, they became more compartmentalized approximately midway through the twentieth century. In the past few decades, there has been a renewed interest in the integration of evolutionary history into ecology and vice versa. Running throughout this literature from a century ago until now has been phylogenetic information in one form or another. This phylogenetic thread constitutes what I call phylogenetic ecology, and it is the topic of this book.

The use of phylogenetic information in ecology is now often touted as a means to integrate evolutionary history into ecology (Cavender-Bares et al. 2009; Cadotte and Davies 2017). However, the ways in which phylogenies have been used in ecology are much more diverse. Phylogenies, or more precisely measures of relatedness, were originally utilized in ecology as proxies for the similarity of species, and a tradition of using phylogenies in this fashion continues to this day in ecology (Jaccard 1901; Elton 1946; Jarvinen 1982; Webb 2000). Phylogenies have also been used in ecology for topics ranging from the inferring of historical biogeography (Brooks 1985; Brooks and Wiley 1986; Brooks and McLennan 1991; Losos 1996; Losos et al. 1998) and the assembly of lineages to considering phylogenetic nonindependence in comparative analyses (Felsenstein 1985; Harvey and Pagel 1991) to quantifying phylogenetic diversity in order to set conservation priorities (Faith 1992, 1996; Baker 2002).

The first goal of this book is to guide the reader through the history of phylogenetic ecology. I begin with phylogenetic nonindependence and comparative methods, despite this not being the first way in which phylogenies were integrated into ecology. I do this and provide a primer on phylogenetic inference at the end of this chapter because a firm understanding of phylog-

enies and comparative methods allows one to properly grasp and interpret that work that led up to these developments and the work since. At this point, I should note that while this book is written primarily for an entry-level researcher that is interested in learning more about how phylogenies have, can, and should be integrated into ecology, it is my hope that the book will also be of interest to the more seasoned phylogenetic ecologist that may or may not appreciate my viewpoint. Thus, I have taken the approach of focusing on core concepts, methods, and topics and major developments. The examples I provide in the text do not constitute a comprehensive treatment of all work on that topic. Rather, I sought to provide a digestible volume that will spur on the interests of a novice reader. I therefore apologize in advance to any colleagues that are dismayed that I did not discuss their work or highlight their work more prominently.

The second goal of this book is to lay out the field of phylogenetic ecology such as it is and then to challenge the field to reconsider how we think about and utilize phylogenies in ecology. My suggestions for a remodeling of phylogenetic ecology arise from my concern for the current state of the field. Over the past decade, phylogenetic ecology has experienced unwarranted euphoria all the way to unwarranted depression. At present, many have pushed phylogenetic ecology aside as a fad or bandwagon that overly relied on phylogenies as a proxy for ecological similarity, while others still believe that phylogenies contain a great deal of useful information that can't be captured via other data sources. I am not convinced that either of these opinions are well grounded (Swenson 2011a, 2013, 2014a). Furthermore, almost all phylogenetic approaches in ecology being employed at present actually fail to do the one thing most say they want to accomplish: integrate evolutionary history into ecology. For example, correlating phylogenetic diversity with an ecological variable is, at best, a weak integration of evolutionary history into ecology, as we know next to nothing about the evolutionary history of the lineages (e.g., the tempo and mode of trait evolution, biogeographic history) and how that history actually impacts ecological interactions. Thus, phylogenetic information should play an important role in ecology, but how phylogenetic information is currently utilized in ecology does not align with this role.

The remodeling of phylogenetic ecology that I propose should have five foci. First, phylogenetic nonindependence or phylogenetic signal in ecological data can be quantified, at least crudely, in most systems of study. This signal should be measured, and phylogenetically informed statistical methods should be employed. Second, measures of phylogenetic diversity are useful for setting conservation priorities and as very quick indicators that something about relatedness is correlated with the ecological pattern or process of

interest. However, phylogenetic diversity itself, no matter how we slice and dice it, will never tell us why phylogeny or evolutionary history is related to the ecological pattern or process of interest. Even in those cases where it is more strongly correlated with a variable other than independent variables, we will not know why, and an assumption that there is a phylogenetically conserved trait driving the relationship is not necessarily true. Third, phylogenies should no longer be used as proxies for ecological similarity. Again, they may give basic initial insights into the diversity in ecological assemblages, but we don't know why a given phylogenetic pattern exists. Fourth, phylogenies are best employed in ecology as backbone pieces of data upon which biogeographic and trait information can be draped. When phylogenies are used in this manner, evolutionary history is truly being integrated into ecology. There is a strong literature that uses the phylogenies in this manner, but it is now often forgotten about in phylogenetic ecology. Fifth, phylogenies are best used for regional- and global-scale studies that elucidate the drivers of regional- and global-scale assemblage composition and diversity. However, we must also strive to elucidate how local-scale ecological interactions feedback to influence these larger-scale processes (i.e., the feedbacks between macro- and microevolution).

If phylogenetic ecology could remodel itself to focus on these five items, then it has tremendous promise to propel the integration of ecology and evolutionary history. A failure to do so will likely result in phylogenetic information being relegated to the backwaters of ecology, where its potential will not be realized. In formulating this remodeling, I have had to confront many issues. First and foremost, I have certainly violated many of the rules I suggest we follow under the remodeling proposed (e.g., Swenson et al. 2006, 2007). Some of this was due to my zeal for using phylogenies, and some of it was due to my desire to obtain more information about the species we study and not being satisfied with only analyzing species names. I do still contend that analyzing species lists and abundance distributions is less powerful than analyzing the phylogenetic composition of ecological systems. However, I have come to realize that phylogenetic information can be better employed in ecology. I have known this for a while, but have been confronted with a second issue. That issue is that the remodeling of phylogenetic ecology requires the generation of phylogenies with dense taxonomic sampling. This is not a trivial problem. Indeed, in some instances, the approaches I suggest almost demand a fully resolved tree of life. We aren't there yet, but the technology, tools, and databases available are getting to a point where well-sampled phylogenies for most to all major lineages in assemblages are possible (e.g., Hinchliff et al. 2015; Kumar et al. 2017). In sum, the remodeling I propose is

not an easy route, but it is, I think, the necessary route for phylogenetic ecology to remain an interesting field of investigation.

1.1. Chapter Breakdown and Progression

The book progresses from phylogenetic terminology, inference, and nonindependence to community phylogenetics and phylogenetic analyses of big data. In the sections that follow in this chapter, I will provide a very simplistic entryway and general introduction to phylogenetic trees for ecologists. Although most students in ecology roughly know what phylogenetic trees do and do not represent, many are hard pressed to explain exactly what data are used to infer them and how they are inferred and interpreted. The goal of these sections is to fill this void and place all readers on the same footing. I will begin with a basic tour of phylogenetic trees, including their structure and specific terminology related to this structure. Once this understanding is achieved, the chapter will move on to give a general overview of how phylogenies are inferred—data types, assumptions, and methods. It is impossible to cover the breadth of phylogenetic theory and inference in a single chapter, and this chapter is not designed to be such a reference. Rather, it is simply meant to set a baseline understanding of how to "read" phylogenies, learn generally how they are made, and recognize what information they do and do not contain.

In chapter 2, we will discuss phylogenetic nonindependence, comparative methods, and the analysis of phylogenetic signal and niche conservatism. Comparative analyses of data from across regions and clades play a critical role in modern ecology, and they have been at the core of many important past developments and syntheses. The robustness of such analyses critically relies on statistical approaches that account for the shared evolutionary history, and therefore statistical nonindependence, of the lineages being investigated (Felsenstein 1985). Phylogenetically informed comparative methods have a long and hotly debated history in ecology (e.g., Ackerly and Donoghue 1995; Harvey et al. 1995; Westoby et al. 1995a, 1995b; Rohlf 2006). There have been many misunderstandings, misconceptions, misapplications of, and downright disdain for phylogenetic information in comparative ecology. I begin the second chapter by discussing, briefly, some of this rocky history and how the lack of phylogenetic information in the past has freed researchers from having to explicitly consider phylogenetic nonindependence in their data sets. However, I quickly transition to the fact that phylogenetic information is now widely available, albeit often in crude form, and should be used in all modern comparative ecology either by using it to analyze data already col-

lected or by using it to design experiments (Weber and Agrawal 2012). I then cover the major classes of phylogenetic comparative methods, the conceptual foundation of the methods, and how they are implemented in practice. The ultimate goals of the chapter are to move the reader away from thinking of phylogenetic nonindependence as a nuisance and toward using powerful phylogenetic comparative methods as a standard approach in their analytical toolbox. Next, I will discuss the measurement of phylogenetic signal and niche conservatism and how and why it has become of interest to ecologists. Throughout this discussion, I seek to link concepts, definitions, and research questions and highlight those instances where, I think, the literature could course correct.

In chapter 3, I focus on the rapidly growing phylogenetic diversity literature. I start with work from the early 1990s where the measurement of phylogenetic diversity became popularized as an additional metric of biological diversity for conservation purposes (Faith 1992, 1996). As phylogenetic information has become more available, measures of phylogenetic diversity, based upon phylogenetic branch lengths, have become more common in the literature (Cavender-Bares et al. 2009). At present, measures of phylogenetic diversity are used as key pieces of information in studies ranging from conservation biology (Vane-Wright et al. 1991; Faith 1992, 1996; Winter et al. 2013) to species coexistence to biodiversity-ecosystem functioning relationships (Cadotte et al. 2008, 2009; Flynn et al. 2011; Srivastava et al. 2012). While phylogenetic diversity itself is fairly easy to conceptualize, in practice there are many metrics of phylogenetic diversity. These metrics can be independent of one another or monotonic, often making it difficult to compare the results of different studies and to achieve a synthesis (Vellend et al. 2011; Swenson 2011b; Tucker and Cadotte 2013; Swenson 2014a; Tucker et al. 2017). This chapter will provide a history of measures of phylogenetic diversity in ecology. An emphasis will be placed on how they are quantified, but more importantly, the text will also explore important conceptual and biological differences between different metrics.

In chapter 4, I discuss one of the two major approaches for integrating phylogenetic information into community ecology, which I term the phylogenetic proxy approach (Swenson 2013). The use of phylogenetic information to understand community assembly and structure has a long history. Early work relied on relatedness as a proxy for ecological similarity, where co-occurring congeners were believed to reflect the importance of the abiotic filtering of similar phenotypes and a lesser role for biotic interactions, such as interspecific competition (Jaccard 1901; Palmgren 1921). This research approach, which computed taxonomic ratios (e.g., the number of genera: the

number of species in a community), led to a rather large literature and some classic debates in ecology regarding the usage of null models (e.g., Simberloff 1970), but it had largely died out by the 1990s. However, Cam Webb's seminal work in the *American Naturalist* in 2000 (Webb 2000), which introduced phylogenetic branch lengths to calculate the degree of relatedness in communities instead of taxonomic ratios, reignited this realm of research, leading to hundreds of articles and the formation of what is now known as "community phylogenetics." The lynchpin of the community phylogenetics research program rests upon the assumption that phylogenetic relatedness is a robust proxy of ecological similarity. Not long after Webb's paper, researchers began to highlight the frequency at which this assumption is not met and the implications of this for inferences regarding the processes driving community assembly and structure (e.g., Cavender-Bares et al. 2004; Losos 2008). The present work describes this entire historical development and discusses the current state of the field of community phylogenetics. Critically, at the end of the chapter, I discuss several major conceptual challenges facing this field and discuss whether the field should hasten its movement away from using the phylogeny as a proxy for similarity and toward using it as a backbone piece of information.

In chapter 5, I discuss the second major approach to integrating phylogenetic information into community ecology, which I call the phylogeny as a backbone approach. The previous chapter covered the historical development and current usage of phylogenetic relatedness as a proxy for ecological similarity in community ecology research. The chapter ends with an argument that in most cases, we should move away from using the phylogeny as a proxy for similarity and toward using it as a backbone onto which we should drape data. Chapter 5 seeks to reinforce and expand this argument by first discussing the development of phylogenetic community ecology where spatial and trait information has been placed onto a phylogeny to make robust inferences regarding the ecological and evolutionary processes underlying the historical assembly and present-day structure of ecological communities. Examples will be drawn from "classic" systems where researchers have successfully and clearly linked evolutionary history with community assembly (e.g., Losos et al. 1998; Gillespie 2004). The chapter will end with an argument that the most interesting and informative future integrations of phylogenetic information into community ecology will come from utilizing phylogenies as backbones and not proxies.

Chapter 6 is a discussion of how phylogenetic information is utilized to ask large-scale ecological questions regarding the drivers of regional- to global-scale patterns of species assemblage composition and diversity. Spe-

cifically, I will discuss the latitudinal species diversity gradient with respect to the niche conservatism (Wiens and Donoghue 2004) and cradles versus museums hypotheses (e.g., Stebbins 1974; Stenseth 1984; Chown and Gaston 2000) and how phylogenetic information is critical for robust tests of these hypotheses. I will also discuss the assembly of regional-scale floras and faunas with respect to the timing of lineage diversification, priority effects, and ecological opportunity. A final goal of this chapter is to elucidate the linkages between phylogenetic analyses at global and regional scales to community-scale analyses that utilize a phylogenies as a backbone approach.

In chapter 7, I discuss an emerging field called functional phylogenomics (Lee et al. 2011), which I think holds tremendous capacity for transforming phylogenetic ecology despite being utilized primarily used in the systematics and evolutionary literature until this point in time. By this point in the book, I will have outlined fundamental limitations in phylogenetic approaches to community ecology as well as standard functional trait inventories of communities. Specifically, the phylogeny is not a reliable proxy of trait similarity, and standard trait inventories do not offer a broad assay of organismal function. Functional phylogenomic approaches offer the opportunity to infer a phylogeny, map gene tree concordance and discordance, and quantify and compare levels of gene family duplication, while providing a broad assay of organismal function. I discuss a few recent examples that have used this approach in evolutionary biology as well as in a community ecology context. I end the chapter with a discussion of future directions for community functional phylogenomics that should be fruitful and feasible for an ecologist to accomplish.

In chapter 8, I discuss the major advances made in phylogenetic ecology catalyzed by informatics tool development. Specifically, in less than a decade the field of phylogenetics has gone from making phylogenetic trees for tens, or occasionally hundreds, of species to inferring trees containing thousands or tens of thousands of species (e.g., Webb and Donoghue 2005; Hinchliff et al. 2015). This development has coincided with the influx of other "big data" in ecology, leading to the emerging fields of ecoinformatics and biodiversity informatics, with the latter being a broader discipline inclusive of evolutionary information such as phylogenies. Thinking about and analyzing big data is becoming so commonplace that most ecologists will need to deal with such data. The chapter covers past and current approaches for inferring large phylogenetic trees useful for ecologists. The chapter ends with a discussion of how phylogenetic imputation techniques (Swenson 2014b) have been utilized in ecology and may be utilized, with appropriate caution, in the future to address the challenge of supersparse ecological data matrices (e.g., Kattge et al. 2011).

The book ends with a chapter recapping some of the major conclusions we can draw from each of the previous chapters and, more importantly, what this means for the future of each of these realms of research, while highlighting key outstanding questions and research trajectories that should be explored. Finally, I will reinforce the argument that phylogenies are incredibly useful structures to consider throughout ecological research programs, and their increasing presence and accessibility in ecology suggests that ecologists should utilize them when necessary to inform their research. Specifically, I will reiterate and discuss the major foci of interest for a remodeling of phylogenetic ecology and how we move forward as a discipline.

1.2. An Introduction and Some Basic Terminology for the Non-phylogeneticist

A phylogeny represents the evolutionary relationships between a group of organisms. In most cases, the organisms are extant species, but this need not always be the case. The relationships are depicted in a graph data structure composed of edges and nodes (fig. 1.1). This structure is often called a topology and often resembles a tree—hence the term "phylogenetic tree." The edges, more commonly called "branches" in phylogenetics, connect a series of internal and terminal nodes. The terminal nodes, also referred to as "leaves" or "tips," represent the organisms—in most cases species. The internal nodes connect the branches. In a fully bifurcating tree, that is, a tree where each internal node gives rise to two branches, the number of internal nodes is equal to the number of terminal nodes (e.g., species) minus one. The earliest internal node in the phylogeny from which all lineages are descended

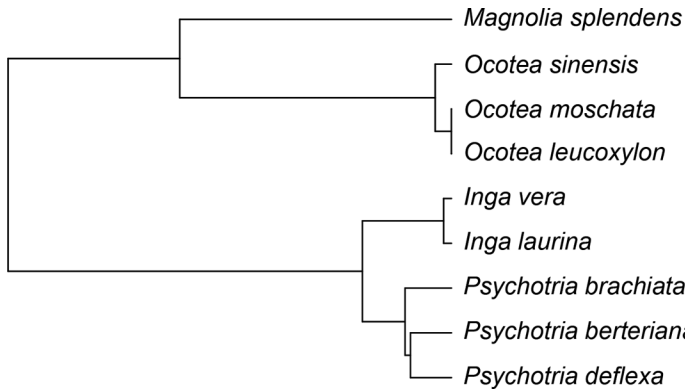


FIGURE 1.1. A hypothetical phylogeny containing nine rain forest tree species. There are nine terminal nodes (a.k.a. leaves or tips) and eight internal nodes, each of which delineates a clade.

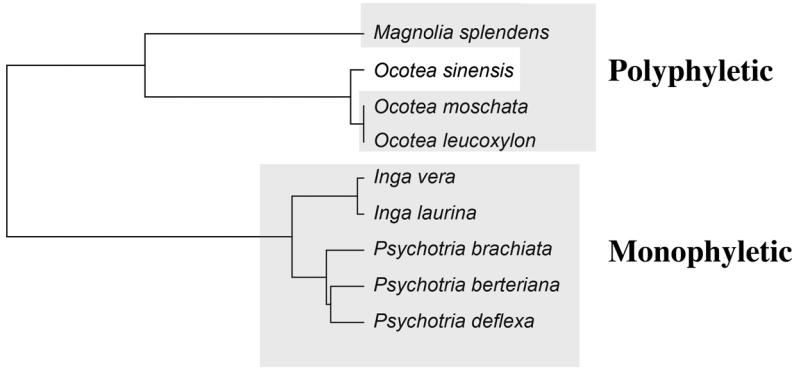


FIGURE 1.2. The same hypothetical phylogeny as in figure 1.1, but with monophyletic and polyphyletic groups shaded. A monophyletic group contains all species derived from an internal node. A polyphyletic group does not contain all species derived from an internal node.

is called the "root" or "root node." In the case where the timing of lineage relationships is unknown, the root node is unknown and the phylogeny is referred to as "unrooted."

Rooted phylogenies are composed of multiple nested clades. A clade is a group of organisms in a phylogeny arising from a common ancestor represented by a given internal node (fig. 1.2). This is a monophyletic group. Thus, the number of clades or subtrees possible from a given rooted phylogeny is equal to the number of internal nodes (i.e., one less than the number of tips). Paraphyletic groups are samples that do not include all tips derived from a common ancestor. Polyphyletic groups are samples that do not include the most recent common ancestor.

Phylogenetic trees can be displayed in a large number of ways (fig. 1.3). A first step after generating or obtaining data is to plot the data. Phylogenetic trees are no different, though plotting moderate- to large-size phylogenies (i.e., phylogenies containing many tips) is a perennial challenge in phylogenetics. Upon first inspection, one of the first patterns one might observe is whether the phylogeny is rooted and whether the tips of the tree all end at the same distance from a root node if it is a rooted tree. Trees where the tips all end at the same distance from a root node are said to be "ultrametric," whereas trees where tips do not all end at the same distance are called "non-ultrametric" trees (fig. 1.4). Next, one might observe whether or not each internal node gives rise to two descendent branches. If it does throughout the tree, as noted above, it may be called a fully bifurcating tree. However, nodes that give rise to more than two descendent branches are called polytomies or polytomous nodes (fig. 1.5). Polytomies represent uncertainty, which we will discuss later in the chapter.

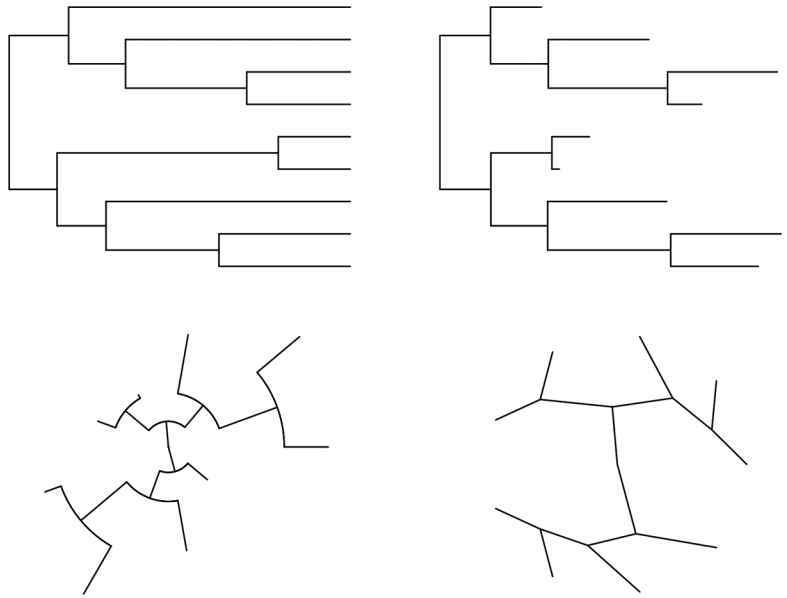


FIGURE 1.3. An example of four different ways in which a phylogenetic tree could be plotted. The upper left is a cladogram simply reflecting the topological relationships. The upper right is a phylogram where branch lengths are scaled to a unit of evolutionary change. The lower left is the same phylogram presented in a circular format. The lower right is the cladogram plotted in a circular format.

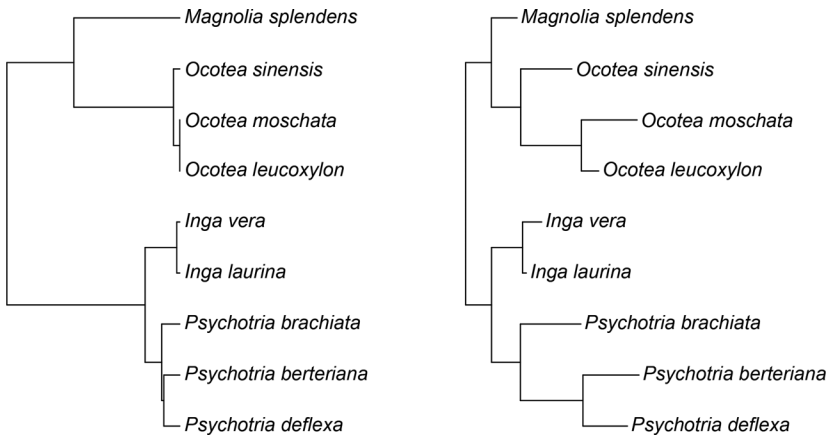


FIGURE 1.4. An example of an ultrametric phylogeny (left) and a nonultrametric phylogeny (right). The key difference is that the terminal nodes (i.e., tips) on the left all end at the same point (i.e., present time).

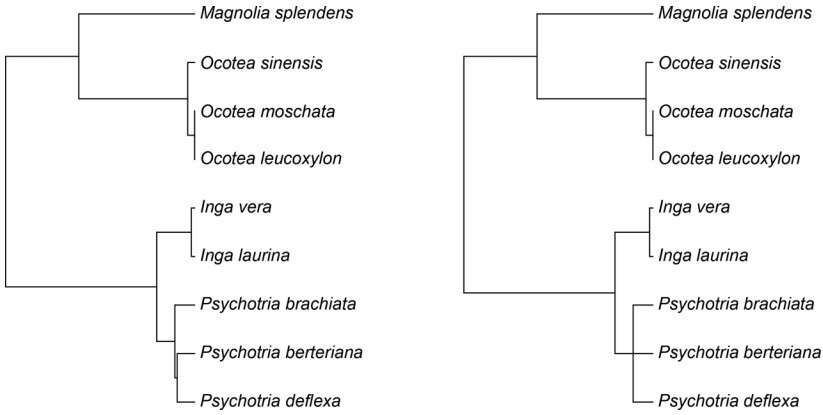


FIGURE 1.5. A fully resolved phylogeny (left) where all internal nodes bifurcate (i.e., split into two branches) and a phylogeny with a single polytomous internal node (right) where the relationships between the three *Psychotria* species are not depicted. This polytomy may be called a soft polytomy if the relationships are simply unknown and a hard polytomy if it reflects a simultaneous three-way split of a lineage (e.g., a large population instantly fragments into three populations that become isolated).

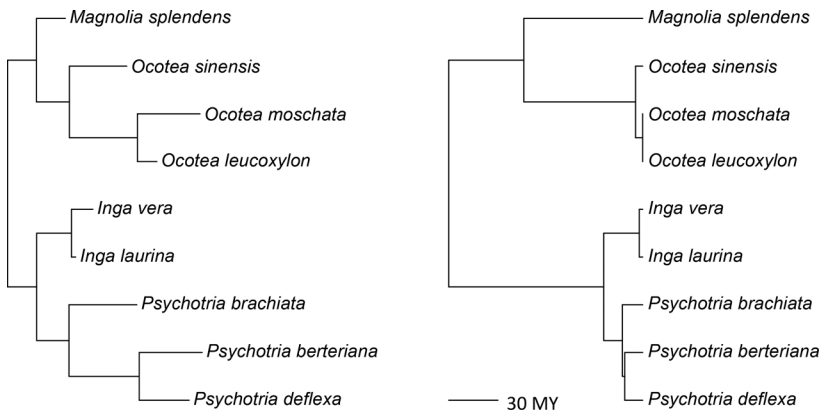


FIGURE 1.6. A hypothetical phylogram (left) scaled to time to produce a chronogram (right). A scale bar is provided to translate branch lengths into units of time (i.e., millions of years). The chronogram in this instance was generated from the phylogram using penalized likelihood.

Next, we may see that the branches within a given phylogeny vary in their length. The length of a branch may represent inferred evolutionary change (e.g., sequence or trait change) or time (e.g., millions of years). In those cases where the branches are scaled to reflect evolutionary change, the phylogeny is referred to as a "phylogram." In those instances where the branches are scaled to reflect time, the phylogeny can be referred to as a "chronogram" (fig. 1.6). If only extant organisms are included as the tips on the phylogeny, then a chronogram will be ultrametric. However, if extant and extinct species

are both included in tips, then the chronogram will be nonultrametric, with the tips for the extinct species ending earlier in the phylogeny than those of the extant species.

A final note on viewing and representing phylogenies that is important to reiterate is that internal nodes can be rotated. Thus, the same exact phylogenetic tree could be drawn in several different ways, making each appear distinct from the others, but they are no different. The differential rotating of nodes can often confuse a non-phylogeneticist even when they understand

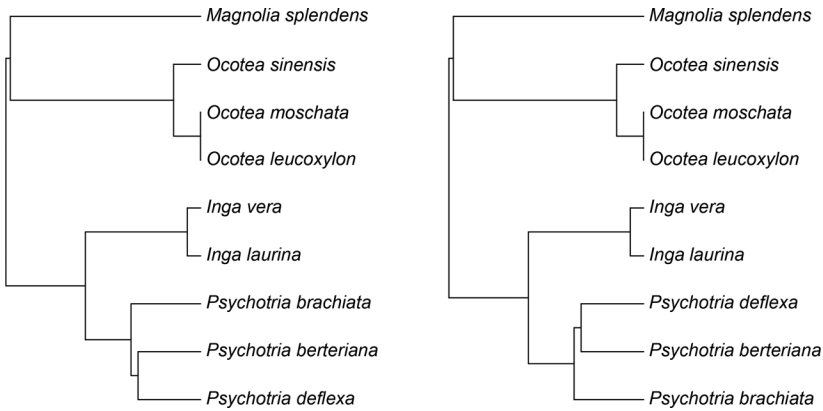


FIGURE 1.7. The same phylogeny plotted in two different ways where the nodes within the *Psychotria* clade have been rotated. Note that the distances between all tips in the phylogeny are the same, and that all *Psychotria* are of equal distance to all other non-*Psychotria*.

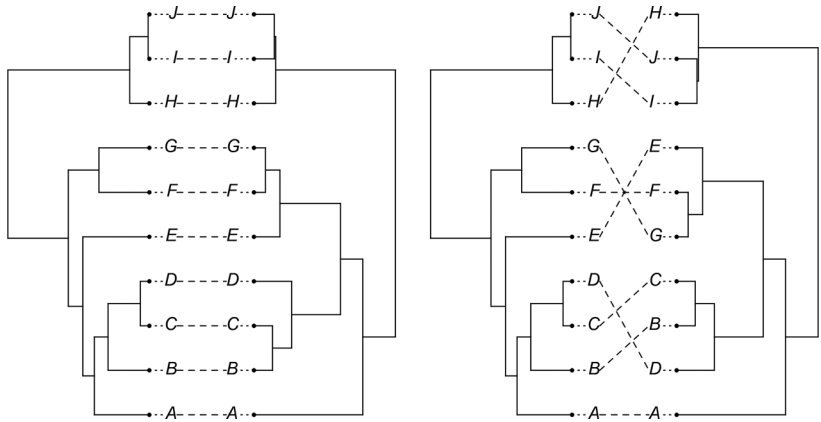


FIGURE 1.8. Two examples of cophylogeny plots. Such plots may be used to compare the evolutionary histories of interacting groups (plants and herbivores, figs and fig wasps, etc.). The degree of concordance may appear different between the two examples, with the left having higher concordance, but they are actually identical. The difference is that the node rotations on the right provide the false impression of less concordance.

that nodes can be rotated. This is particularly true when it comes to thinking about the degree of relatedness of species. For example, in a given chronogram containing only extant species, two sister species are equidistant from all other species in the phylogeny (fig. 1.7). This rotation of nodes is also important to recall when comparing two phylogenies, such as when one is considering the codiversification of two groups (e.g., plants and lepidopterans) (fig. 1.8). Thus, caution is warranted when assessing the topology of a phylogeny that one generates or is given.

1.3. Phylogenetic Inference: The Data and Methods

In this section, I will briefly cover the topic of phylogenetic inference. The goal is to give you, the reader, a primer on the topic such that it is clear what data, methods, and assumptions are utilized during phylogenetic inference. The goal is not a comprehensive treatment of these topics. Those interested in pursuing a research program in phylogenetic ecology long-term will want to become more intimately familiar with phylogenetic methods and are advised to read the most exhaustive text on the topic by Felsenstein (2004) and the detailed, but more accessible, text by Baum and Smith (2013).

We begin with the simple reiteration that phylogenetic trees are hypotheses, are inferred, and that the "true" phylogenetic tree is unknown. Thus, there is no one true and stable phylogeny that will be utilized for all analyses ad infinitum. As new data and approaches become available, the inferred relationships and distances between organisms will change. Furthermore, in many cases a series of phylogenetic hypotheses are equally supported given the data and methods currently at hand.

The data utilized for phylogenetic inference may be termed characters. The data are stored in a data matrix typically with different characters in the columns and the organisms (e.g., species) in the rows. In ecology, we may simply refer to this as a trait matrix. Indeed, in the past, character matrices used in phylogenetics were trait matrices and the characters selected for measurement were generally believed to have phylogenetic signal. This may be contrasted with traits that are likely to evolve quickly. Classically, traits of ecological importance were believed to be the latter of the two types of traits, but as discussed by Donoghue (2008), the more ecologists have measured phylogenetic signal in the traits they measure, the more they find it. Presently, most phylogenetic inferences use multiply aligned DNA sequence data as the character data with a single site per column (fig. 1.9). There are four main classes of methods that could be used for phylogenetic inference from a character matrix—maximum parsimony, distance based, maximum

Species								
Species 5	A	C	C	A	T	G	G	T
Species 4	A	T	C	A	T	G	G	T
Species 3	A	T	C	A	G	G	G	T
Species 2	A	T	T	A	T	T	A	C
Species 1	T	G	T	C	A	T	C	A

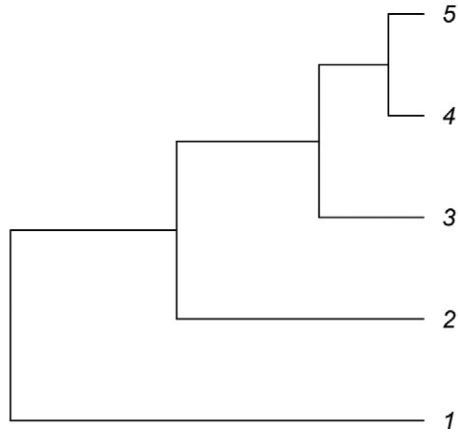


FIGURE 1.9. A hypothetical aligned DNA sequence matrix composed of eight sites (columns) and five species (rows). The matrix was used along with maximum parsimony to generate the plotted phylogeny.

likelihood, and Bayesian. We will step through each of these focusing on inputs, outputs, advantages, and disadvantages.

Maximum parsimony seeks to reconstruct a bifurcating phylogenetic tree that requires the smallest number of character changes. In figure 1.10, I give an example of two phylogenies containing the same five species while considering a signal categorical trait (i.e., flower color). I show two possible reconstructions: one where the blue flower color has evolved only once and another where it has evolved multiple times. The first reconstruction is the more parsimonious of the two. This can be quantified by calculating the tree length, which is the number of character state changes required in a given tree where the lowest length is the most parsimonious. This parsimony approach can be calculated across all characters in the data matrix. The characters can be equally weighted (i.e., Fitch parsimony; Fitch 1977), or differential weighting (i.e., weighted parsimony; Farris 1969) can be applied across characters to assign relatively more importance to one character (e.g., flower symmetry) over another (e.g., flower color). Similarly, changes within a character can be differentially weighted such that two different character state changes have two different costs, thereby making one type of change (e.g., nucleotide transitions) less costly and, therefore, adding less to the tree length than

another type (e.g., nucleotide transversions). In many cases, these weighting decisions within and among characters may be obvious or intuitive to the investigator given their biological understanding of the system. However, even in these cases, the relative ordering does not provide a final weighting (i.e., how much harder it is to transition from pink flowers to blue flowers than it is from pink flowers to red flowers). Thus, at the end, the investigator is ultimately making weighting decisions that may seem arbitrary, or they are forced to weight all characters and changes in character states equally, which is unrealistic. Parsimony reconstructions are among the faster techniques for tree inference partially because they only search for the topology that has the lowest tree length.

Distance-based methods begin with quantifying the distance between all organisms in the sample (i.e., the rows in the character matrix) given the character data. For example, the Euclidean distance of each pair of species could be calculated in multivariate trait space to produce a pairwise distance matrix. In the simplest case, a nucleotide change between species at a site in the character matrix may be assumed to be equally likely (i.e., equally weighted). This model is called a Jukes–Cantor model of sequence evolution, where the difference between transitions and transversions is ignored (Jukes and Cantor 1969). Distance-based methods often use a Jukes–Cantor assumption to arrive at an evolutionary distance matrix given a DNA sequence character matrix, which is then used with neighbor joining to produce a first

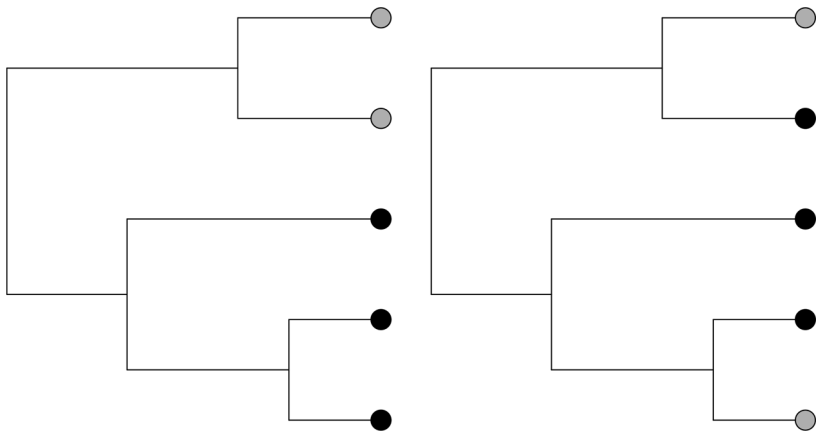


FIGURE 1.10. Two hypothetical phylogenies containing five species. The terminal nodes are colored according to a categorical trait—here, flower color. On the left, one character state transition has likely occurred where the root may have been the black state and a single transition to the gray state occurred. On the right, at least two character transitions have occurred: from black to gray in the clade of three species, and from black to gray again in the clade with two species. Thus, the phylogeny on the left has fewer inferred transitions and would be a more parsimonious topology given the character data.

glance at the possible relationships between species. In this approach, both a topology and branch lengths are produced, but the result is a single phylogeny that is not compared to alternatives. This makes neighbor joining with a Jukes–Cantor model extremely fast, but it also makes it very limited and therefore only useful for a first look at the data.

Phylogenetic inference using maximum likelihood is the process of finding the phylogenetic tree, considering both the topology and branch lengths of the tree, that is most probable given the DNA character matrix and a model of DNA sequence evolution. We have already covered the Jukes–Cantor model of sequence evolution where all character changes at a site are equally probable. This basic model is flawed in a number of ways, which gives rise to more biologically reasonable models that come at the cost of increasing the number of parameters in the model. The first modification to the Jukes–Cantor model is relaxing the assumption that all nucleotides occur at equal frequency. Felsenstein (1981) proposed a sequence evolution model that weights each nucleotide by an expected frequency, where all nucleotide frequencies sum to one, such that the potential change of one nucleotide to another is weighted by the expected frequency of the new nucleotide. Next, Hasegawa et al. (1985) refined this model to account for transition versus transversion biases. Specifically, transitions (G → A, T → C, etc.) are modeled to be more likely than transversions (G → C, A → C, etc.), but each type has a single weighting parameter. Finally, general time-reversible (GTR) models extend the model to allow for differential rates among the transversions and among the transitions such that a total of six different rates (instead of two in the previous model) are possible. Each of these models, from Jukes–Cantor to GTR, are time reversible, such that changes from A → T → A are possible. Furthermore, each model can be modified to include a site to site rate heterogeneity parameter (generally called gamma) that allows for differential rates of sequence evolution across sites. Competing models of sequence evolution can be considered in light of the character matrix, while penalizing for the number of free parameters, and the best fit model can then be used in the maximum likelihood tree inference where the most probable tree given the character matrix and model of sequence evolution is sought. This search is conducted by calculating the likelihood of each character given a phylogeny, quantifying the likelihood of a phylogeny by multiplying character-specific likelihoods given the phylogeny, optimizing the parameters to maximize likelihood, and finally comparing the log-likelihood of the phylogeny against other candidates with higher (i.e., least negative) log-likelihoods being preferred. It is important to note that the log-likelihoods of multiple phy-

logenetic trees may be so similar that they cannot be significantly differentiated (i.e., there is no significant log-likelihood ratio between two trees). Thus, there is often not one tree resulting from these analyses.

Bayesian phylogenetic inferences use Bayes's theorem to ask what is the probability that a phylogeny is true given character data (Baum and Smith 2013). The numerator in the theorem is the product of likelihood of character data given the phylogeny (i.e., the phylogeny likelihood just discussed) and the prior probability of the tree. The prior probability of the tree in many cases is unknown, and a flat prior is utilized, which is equivalent to one over the number of possible topologies given the number of tips. The denominator in the theorem is the probability of the data, which requires the consideration of all possible phylogenetic trees. The very large number of possible trees makes this effectively impossible. Therefore, Markov chain Monte Carlo (MCMC) algorithms are used to search tree space in an informed way to compare the log-likelihoods of phylogenies to, hopefully, generate a stable posterior distribution of phylogenies that are most probable given the character data.

Now that I have, very briefly, sketched out the different methods used for tree inference, I will discuss levels of clade support. The above inference routes may result in one to many trees. These trees may be the "best" given the data, but we would still not know the level of support for individual clades within this topology or these optimal topologies. The most commonly encountered approach for measuring clade support is nonparametric bootstrapping. Bootstrapping is the repeat sampling of something with replacement. In this context, we are sampling the columns of the character matrix with replacement until the number of samples equals the number of columns in the original character matrix. Thus, a character can be represented multiple times, once, or never in the newly generated character matrix. This new character matrix is used to generate a new phylogenetic tree. The monophyly that defines each clade in the original tree is compared to the new tree to see if the monophyly is supported. This is then repeated many times (e.g., 100 iterations), each time creating a new character matrix and phylogenetic inference and comparing the topology to the original. If the original clade is found in 95 out of the 100 new phylogenies, then a bootstrap score of 95 is assigned to that clade, indicating strong support. If it is only found in 15 out of the 100 new phylogenies, then a score of 15 is assigned, indicating that the support for this clade is very low. In those cases where clade support is low, the clade may be collapsed into a soft polytomy where more than two branches arise from an internal node with low support (i.e., the node is no

longer bifurcating). Soft polytomies contrast with hard polytomies, which are internal nodes where more than two branches arise due to a rapid simultaneous diversification of an ancestor into three or more lineages.

Parametric bootstrapping is slightly different in that it uses the original tree, usually from a maximum likelihood analysis, and a model of sequence evolution to simulate completely new data. Specifically, a random sequence is evolved one site at a time along the branches of the tree and given the model of sequence evolution. The resulting data matrix is then used to infer a new phylogeny. This process is repeated many times (e.g., 100 iterations), and clade support can be measured just as is done with nonparametric bootstrapping via a bootstrap score. Additional methods that can be found in the literature are the comparison of topologies for different DNA matrix partitions or gene trees, but we will not discuss those presently.

1.4. The Tree, a Forest of Trees, and Living with Uncertainty

We have seen that phylogenetic inference methods can result in one tree, a series of equally likely trees, or a posterior distribution of trees. Even in those cases where a single tree is produced (e.g., neighbor joining), levels of support for clades within the tree will vary. Layered on top of this uncertainty is that phylogenies are only representing hypothesized relationships between organisms and the true relationships will remain forever uncertain. This uncertainty clashes with language often used in the literature regarding "the phylogeny" or "the tree." The real tree is unknown, often there is a distribution of trees produced by an analysis, and there are different degrees of support for clades within the tree or trees produced.

Referral to the phylogeny or the tree for a study system may simply be shorthand language, or it may reflect a lack of understanding. However, the analysis of just one phylogeny is another matter. Frequently in the ecological, and even the evolutionary, literature, the analyses are conducted using a single phylogeny. In phylogenetic ecology, this is almost always the case. Furthermore, phylogenetic ecology generally does not even consider levels of support for clades within that tree. This raises several important questions. How is this single tree selected for analysis over the other, equally probable trees? Why are levels of support not considered? How sensitive are the derived inferences to the selection of one of many equally probable trees?

Phylogenetic ecology has not progressed very far in dealing with the above questions and the consideration of a forest of trees and uncertainty rather than a single representative tree. My suspicion is that this lack of progress partially comes from a lack of understanding regarding phylogenetic inference

methods and, to a greater degree, a lack of computational methods, time, or power to conduct the analyses across a distribution of trees. Hopefully, the previous sections have helped remove this first issue. I can appreciate this second issue, as there have been many times in my work where it has been difficult to conduct the analyses on even a single phylogeny or I have only had access to a single phylogeny. However, Moore's Law continues to march forward, and the computational power that can be employed by a researcher is growing immensely year after year. This expanding computational capacity means not only that larger phylogenetic trees can be inferred, but also that we have the ability to conduct our analyses across distributions of trees and with consideration given to levels of clade support. The reader will see that I will raise this issue in multiple places in this book, and I hope that it will serve to nudge phylogenetic ecology toward a higher frequency of sensitivity analyses that consider the forest of phylogenetic trees and uncertainty.

2

Phylogenetic Nonindependence, Comparative Ecology, and Phylogenetic Conservatism

Ecologists have traditionally made their first analytical encounter with phylogenies as something that must be considered when conducting comparative analyses (Harvey and Pagel 1991). Over the past decade, this has become less and less true where phylogenetic information is utilized for measuring biodiversity and inferring ecological mechanisms (Faith 1992; Webb et al. 2002). However, before delving into how phylogenetic information is utilized in those contexts, it is useful to consider the foundational work relevant to ecology that has become the phylogenetic comparative methods literature. This literature can be challenging for novices and experts alike for a variety of reasons. First, it is a large and fast-moving literature, with methodological and conceptual tweaks being continually published along with totally new approaches being developed frequently. Second, it is a literature that is littered with strong opinions and acrimonious debates. While ecologists are no stranger to such issues, as an outsider, it can be difficult for an ecologist to determine why one method should or should not be preferred, whether metrics are slightly different or night-and-day different, and whether any of this matters for addressing an actual biological question or whether some of it is simply a collection of obtuse arguments about semantics that has nothing to do with the actual biology of interest. Given these issues, I am aiming to provide a gentle introduction to this literature for the novice. I have not attempted to provide a comprehensive overview of the comparative methods literature, and I have tried to stay away from intense (and often important) methodological and conceptual arguments. These limitations can frustrate the phylogenetically knowledgeable reader, but I do not believe they will hinder the growth of the novice. Rather, by focusing on the basics, I hope to en-

tice the novice to keep digging into the literature beyond that covered in this chapter rather than scare them off comparative methods forever.

The chapter begins with the foundation of the comparative methods literature—phylogenetic nonindependence. I provide a brief conceptual overview of the problem and how ecology has struggled, accepted, and ultimately gladly embraced it. From a historical perspective, it is fascinating to observe how ecology went from being forced to account for phylogenetic nonindependence and begrudgingly including it in their analyses to searching for phylogenetic nonindependence and having it be a major research objective. It is at the point now that an ecologist will look for phylogenetic nonindependence and be happy to have found it! I will discuss whether this development has been a good thing and how ecology can slightly adjust the course of investigation to make the measurement of phylogenetic signal more compelling and useful for advancing ecology. I end the chapter with a very brief overview of the core classes of phylogenetic comparative methods that an ecologist might encounter in the literature. Again, this is meant to be a brief and incomplete overview to help the novice dip their toes in the water.

2.1. Nonindependent by Common Descent and a Community Dealing with a Statistical Nuisance

All species on the planet share a common ancestor and are related to varying degrees. Common descent and trait heritability are cornerstone concepts in evolutionary biology and dictate that species are nonindependent entities. Furthermore, descent with modification should produce varying degrees of nonindependence such that, all else being equal, closely related species are expected to be more similar (i.e., nonindependent) to one another than distantly related species, due to a more recently shared common ancestor (Darwin 1859). In short, species are nonindependent and the degree of this nonindependence is expected to be dependent upon their degree of relatedness (Felsenstein 1985; fig. 2.1).

The importance of independent and identically distributed random variables is burned into the brains of students in introductory statistics courses. If the data violate these assumptions, then a separate class of methods should be considered and applied. Ecologists frequently encounter such issues in their data, with spatial autocorrelation perhaps being of the greatest concern to most (Legendre 1993; Peres-Neto 2009). However, phylogenetic autocorrelation (i.e., nonindependence) is likely as common in ecological data sets (Harvey and Pagel 1991; Donoghue 2008).

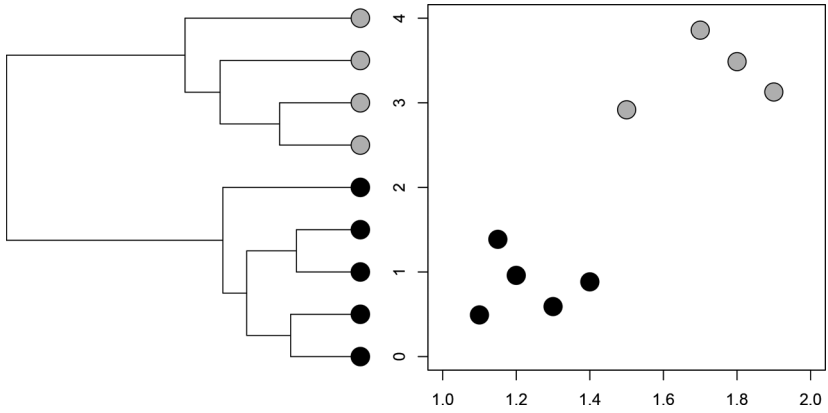


FIGURE 2.1. A simple graphical example of phylogenetic nonindependence. On the right is an *x-y* plot of values for two traits from nine species. Plotted without respect to phylogeny, it would appear there is a strong coordination between the traits and that they may have even evolved in a correlated manner. However, when considered in light of the phylogeny, we can see that a simultaneous change in both traits at the first bifurcation in the tree generates the overall pattern and that subsequent changes in one trait within the two major clades did not mean a change in the other trait in the expected direction.

The prevalence of and how to deal with phylogenetic nonindependence has been (unnecessarily) controversial in ecology for decades. The description and possible solutions to the problem of phylogenetic nonindependence were best described to comparative ecologists by Felsenstein (1985) and Harvey and Pagel (1991). Important outcomes of these works are the description of how independent contrasts may be derived and analyzed and detailed discussions of phylogenetic nonindependence and how it may be interpreted. More specifically, Felsenstein (1985) developed methodology permitting correlations of trait values across a sampling of species with phylogenetically informed degrees of freedom and Harvey and Pagel (1991) discuss multiple ways in which data may be phylogenetically nonindependent and how to conceptually and methodologically confront said data. Despite these advances, phylogenetically informed statistical methods in comparative ecology were frequently not utilized or only begrudgingly utilized in the literature. The issue came to a head in a classic argument in the plant comparative ecology literature in 1995.

An investigation into seed size in temperate zone floras by Lord, Westoby, and Leishman published in the *American Naturalist* (Lord et al. 1995) was the genesis of a debate regarding when and if phylogenetic comparative methods should be utilized in comparative ecology. Specifically, in a Forum in the *Journal of Ecology*, Westoby et al. (1995a) argued that what they termed the "phylogenetic correction" was often misapplied or misinterpreted in the

comparative methods literature. Their argument was largely based on the notion that variation in traits is partitioned into phylogenetic and ecological components as well as their intersection when one applies a phylogenetic correction. When there is a large correlation between the ecological and phylogenetic components, which often occurs in comparative data sets, they argued that researchers were biased toward attributing the results to phylogeny rather than ecology. Furthermore, they argue that phylogeny and ecology are not mutually exclusive and that ecological interactions can leave a phylogenetic signal in data. Harvey et al. (1995) countered this argument by pointing out that the most current methods do not seek to partition variation in the manner described by Westoby et al. (1995a; fig. 2.2). Rather, they were more concerned with dealing with the nonindependence of data and using biologically reasonable degrees of freedom. Furthermore, they argued that it was incorrect to suggest that those promoting phylogenetically informed comparative methods believed that phylogenetic signal arose independent of ecology and that, as Harvey and Pagel (1991) had pointed out, there are multiple reasons why phylogenetic nonindependence may occur in data. A third contribution by Ackerly and Donoghue (1995) took the role of mediator between the two sides of the argument, highlighting that current phylogenetic methods are not a correction, but there may be a tendency to incorrectly infer a lack of ecological interactions when there is a strong phylogenetic signal in data, and the intersection of phylogenetic history in trait evolution and ecology is an exciting area for future research and not simply a nuisance or something that must be corrected in data sets.

This argument was, and is, important to the development of phylogenetic

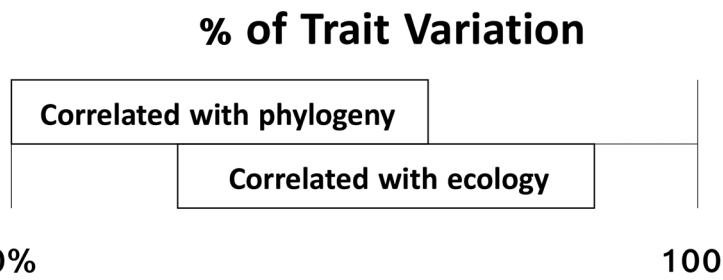


FIGURE 2.2. A graphical depiction of the issue raised by Westoby et al. (1995a) where trait variation is partitioned into a phylogenetic component, an ecological component, their interaction, and unexplained variation. Westoby et al. (1995a) argued that some may erroneously call the phylogenetic and phylogenetic-ecological interaction all phylogenetic. It is debatable whether this is actually what contemporary researchers were doing at the time (Harvey et al. 1995), and a phylogeny-ecology dichotomy seems unwarranted from my perspective, as ecological interactions impact macroevolutionary outcomes and vice versa (Swenson 2011a).

ecology for multiple reasons. First, it demonstrates the strong resistance to comparative methods that was very common one to two decades ago, which is less common today. Second, it highlights how phylogenetic biologists and ecologists would often talk past one another, failing to see the valid concerns of the other. Finally, the contribution of Ackerly and Donoghue (1995) proved to forecast the future of phylogenies in ecology, touching on the importance of phylogenetic niche conservatism, appropriate usage and interpretation of comparative methods, and the advantages, rather than the disadvantages, of using phylogenies to unravel major questions in ecology. Within ten years, the Ackerly and Donoghue (1995) vision of phylogenetic ecology was beginning to be fully implemented, to the point where it is now widespread (Webb et al. 2002). However, during the 10-year interim, phylogenetically informed analyses were still relatively rare in ecology. A major driver of this absence can be attributed to ecologists not having access to phylogenies containing the species in their systems. Thus, a lack of phylogeny excuse was invoked where phylogenetically informed analyses may be more appropriate and interesting, but they are not possible due to a lack of phylogeny. In the next section, I will discuss this excuse past and present.

2.2. The Lack of a Phylogeny Excuse: Then and Now

The discussion surrounding phylogenetic nonindependence in comparative ecology was dismissed by many for decades as a largely conceptual or philosophical exercise with little to no impact on how one conducted their analyses. Phylogenetic nonindependence, no doubt, was and still is a concern frequently raised by grant and manuscript reviewers. However, most ecologists lacked a phylogenetic tree linking the species in their study system, thereby partially preventing them from using the phylogenetic comparative methods that were being developed at the time. Thus, not having a phylogenetic tree became an excuse for not incorporating phylogenetic nonindependence into an ecological analysis.

In reality, the lack of a phylogenetic tree depicting the relationships of species in an ecological study was never truly a valid excuse for not considering the nonindependence of species in almost all cases. The taxonomic hierarchy itself could be used to represent the relatedness of species while realizing the potential biases introduced by missing internal nodes and not knowing the branch lengths separating taxonomic levels. If one did not wish to utilize a cladogram based upon taxonomic ranks for their study, taxonomy could be utilized to partition variation in the data collected to, at minimum, indicate the amount of variation in the data in the different nested taxonomic levels

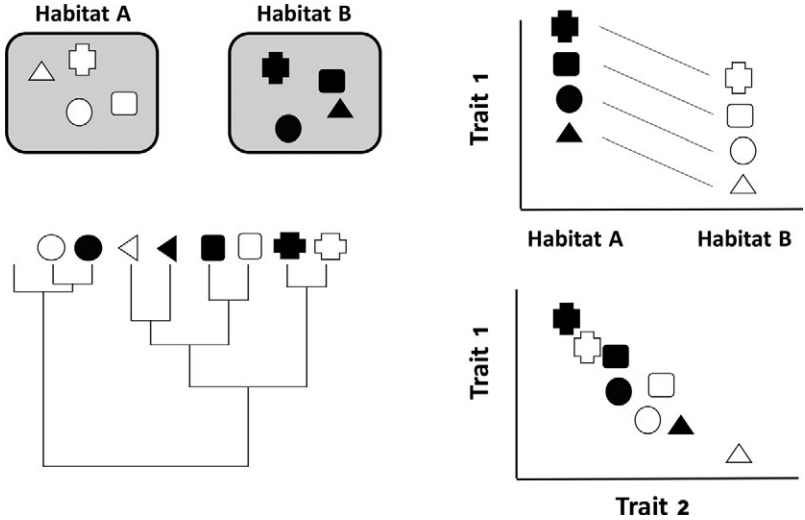


FIGURE 2.3. A paired species research design. Here, four pairs of species from four different clades (e.g., genera) are chosen for comparison. In one scenario, one representative has a preferred habitat or categorical trait and the other representative has another. Trait differences are compared between the pairs (upper right panel) to quantify whether a change in the categorical variable is associated with a change in the continuous trait. The lower right figure shows data for two continuous traits. Here, there is phylogenetic signal in the traits (i.e., the triangle clade has the lowest trait 1 values and highest trait 2 values), but the traits change in a coordinated fashion between each pair, which is what phylogenetically independent contrasts (Felsenstein 1985) would elucidate.

(e.g., Kerkhoff et al. 2006). Additionally, congeneric species pair comparisons were and are a quick and easy approach for reducing the nonindependence in a comparative ecology study (Swenson 2009b; Weber and Agrawal 2012; fig. 2.3). Perhaps the only cases where structuring a comparative ecology study or analysis by phylogenetic information would be challenging, if not impossible, would be where the researcher only had morpho-species names. For example, imagine a researcher dropped into a tropical forest and was completely unfamiliar with the flora and not even able to identify individuals to the order, family, or genus level, but was able to measure traits on individuals grouped into what they believed were visibly distinguishable units called morpho-species. This researcher would, therefore, have no taxonomic knowledge and therefore no knowledge regarding the phylogenetic nonindependence of the samples. In this case, the researcher may be free from being criticized for not considering a sampling or experimental design that considers phylogenetic nonindependence. However, we might still be able to criticize them for not being able to identify plants to even orders or families! Such instances are likely to be exceedingly rare in ecology. In sum, the lack

of a phylogenetic tree has been used in the past to justify not accounting for phylogenetic nonindependence in ecological data sets, but viable alternatives exist, indicating this was not a valid excuse.

2.3. Phylogenetic Conservatism and Signal: Fumbling around with Conceptual Descriptions

The term "phylogenetic conservatism" had been used at the inception of the comparative methods literature to mean the tendency of closely related species to be more similar to one another than they are to distantly related species (Harvey and Pagel 1991). This concept was represented quantitatively using a Brownian motion model of trait evolution (Felsenstein 1985). However, this conceptual and quantitative description for the term "phylogenetic conservatism" has been redefined or conflated with other terminology over the past decade, leading to often-imprecise discussions regarding a pattern of phylogenetic conservatism and the processes that may underlie it (Blomberg and Garland 2002; Swenson 2011a). In the following, I venture to quickly disentangle this terminology conceptually and quantitatively with the expectation that it will allow a beginning phylogenetic ecologist to navigate the growing phylogenetic conservatism literature.

In phylogenetic ecology, the confusion regarding what researchers mean by phylogenetic conservatism can be tracked back to at least Peterson et al. (1999). The confusion may well have had an earlier nexus, but this particular work is historically important due to its outsized influence on the phylogenetic conservatism discussion. This influence was partly due to the novelty of the study, publication in a prominent journal, and confluence of macroevolutionary thinking with an ecological niche modeling literature that was just beginning to skyrocket with Peterson et al. at the forefront. Briefly, the Peterson et al. (1999) study asked whether ecological niche models constructed using data for a species of bird, mammal, or butterfly could accurately predict the ecological niche of a sister bird, mammal, or butterfly taxon in southern Mexico. The researchers found that successful predictions could be made below the family level, which they termed "niche conservatism." The idea of comparing the similarity or overlap in niche space between pairs of closely related species soon took off, with prominent niche modelers and phylogeneticists expanding on the approach of Peterson et al. (1999). For example, Graham et al. (2004) generated a framework for inferring the geographic and ecological mode of speciation for closely related species based on their geographic overlap and similarity in ecological niche space. An outcome of

this explosion of research activity surrounding ecological niche models was a rapid growth in the use of the term "phylogenetic niche conservatism."

By 2005, there was enough interest in phylogenetic niche conservatism and a deep enough literature on the topic that John Wiens and Catherine Graham produced a detailed review on the topic of niche conservatism (Wiens and Graham 2005). The first line of the abstract of their review paper provided a definition of niche conservatism. Specifically, they state: "Niche conservatism is the tendency of species to retain ancestral ecological characteristics" (Wiens and Graham 2005). This definition lines up with the conceptual and quantitative approach that Peterson et al. (1999) had toward niche conservatism as well as that used by researchers predating Peterson et al. (e.g., Ricklefs and Latham 1992) and the rest of the ecological niche modeling research community. This definition, however, does not align well with that used in the comparative methods literature. Specifically, Wiens and Graham use the word "retain," indicating that two sister species, for example, will have the same niche as their ancestor and one another or the same trait as their ancestor and one another if we extend their concept to discuss "trait conservatism." The phylogenetic comparative methods literature uses wording such as "similarity" or "dissimilarity" between species dependent upon their degree of relatedness, shared branch lengths, and so on. In other words, niches or traits could be conserved from the opinion of a phylogenetic comparative methods researcher even if sister species did not share identical traits or niches and are divergent from their ancestral state. The difference in these definitions is far more than a case of semantics. The Wiens and Graham (2005) definition for conservatism, in essence, is evolutionary stasis, while the comparative methods definition is, in essence, evolutionary drift. The evolutionary and ecological processes and patterns consistent with these definitions are very different. This has led to a great deal of confusion in the literature, whether authors and readers realize it or not.

A similar scenario has occurred in the macroevolutionary literature regarding the terms "phylogenetic inertia," "phylogenetic constraint," "phylogenetic conservatism," and "phylogenetic signal." This confusion is nicely described and sorted out by Blomberg and Garland (2002). They provide a nice historical treatment highlighting times where authors have used these terms as synonyms or not, and the confusion that has resulted in the literature. For example, the term "phylogenetic inertia" alone could mean to a researcher no trait evolution, which may be consistent with phylogenetic constraint, or continued drift or differentiation in a trait with time since divergence. Fortunately, the terms "phylogenetic inertia" and "constraint" have

not seeped deeply into the phylogenetic ecology literature, and we are less burdened by this additional terminological and conceptual baggage.

The above hopefully serves to demonstrate that the concept or term of phylogenetic conservatism appears to be of interest and foundational for many, and that we all may think we know what it is, but we often define it in very different ways. In the past, I have tried to help ecologists through this morass by attempting to reset our conceptual definitions for specific terms (Swenson 2011a), and I will do so again presently. First, I suggest that the terms "phylogenetic niche conservatism" and "phylogenetic conservatism" should be used *sensu* Wiens and Graham (2005). That is, they should be used to reflect a lack of trait or niche evolution. This is not to say that Wiens and Graham are "right" and others have been "wrong" in how they use these terms. Rather, I make this suggestion because the word "conservatism" does indicate retention or the lack of decay of a state. Furthermore, the Wiens and Graham (2005) definition appears to be the one most ecologists have in mind when they think of phylogenetic conservatism, particularly those not very familiar with phylogenetic comparative methods. So, where does that leave us with respect to the Brownian motion model definition? In step with the current comparative methods literature (e.g., Blomberg et al. 2003) and much of the phylogenetic community ecology literature, I suggest ecologists use the term "phylogenetic signal."

The benefit of using these two suggested terms is that they also both have clear quantitative definitions: no trait or niche evolution for "phylogenetic conservatism" and trait or niche evolution consistent with the expectations of a Brownian motion model. What should be immediately obvious is that most data should fit neither of these definitions. Phylogenetic niche conservatism, in particular, seems very unlikely. It seems likely that several traits or niche axes may not diverge between sister species (Sobel et al. 2010). However, if we utilize a biological species concept and assume they are reproductively isolated, then it is easily argued that one to many reproductive niche axes are not conserved and therefore the overall niche is not conserved. Thus, it might be more useful to discuss niche axes or traits that are conserved, and to eschew the idea that the entire niches of two sister species completely overlap. Similarly, finding a pattern of trait evolution that perfectly matches a Brownian motion expectation will be very uncommon. Fortunately, continuous metrics exist for how closely a pattern of trait evolution approaches a Brownian expectation. In other words, it is possible to quantify shades of gray or the degree of phylogenetic signal rather than have a binary definition of conserved or not or signal or not. In the following section, I will outline

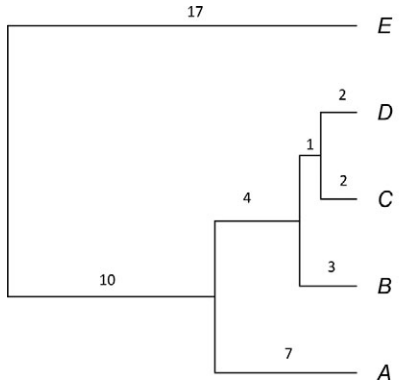
two widely used quantitative approaches for measuring the amount of phylogenetic signal in continuous trait data.

2.4. Measuring and Interpreting Phylogenetic Signal

The tendency of related species to be more similar to one another than distantly related species is a general definition of phylogenetic signal. We contrasted this with a definition of phylogenetic conservatism that indicates no difference between related species. In other words, under this framework, when discussing phylogenetic signal, sister species can be similar, but not exactly the same (i.e., some trait evolution), whereas conservatism indicates sisters are identical (i.e., no trait evolution). The next goal is to provide a quantitative definition and methodologies for measurement of phylogenetic signal.

We will begin with defining a phylogenetic variance-covariance (pVCV) matrix that will serve as a centerpiece for both methodologies we will discuss. The pVCV matrix is a square matrix with the tip names from a phylogeny, generally species names, arrayed across the rows and columns of the matrix (Felsenstein 1985). The off-diagonal elements represent the amount of shared branch length between two species. In other words, these elements represent the amount of shared evolutionary history between two species. Similarly, the diagonal elements reflect the amount of shared branch length, but in this instance, it is a conspecific comparison such that the value simply reflects the distance from the root to the tip of the branch. When the phylogeny being analyzed is ultrametric, the structure of the pVCV is easier to understand and the off-diagonal elements become easily comparable (fig. 2.4). For example, the distance from the root to any tip on the phylogeny will be the same, such that the diagonal elements will all have the same value. Furthermore, the off-diagonal element representing the amount of shared evolutionary history between any two species can be subtracted from the diagonal elements to calculate the amount of branch length since the most recent common ancestor for the two species. In other words, the off-diagonal represents the amount of time the two tips were sharing history, and this value minus the diagonal element represents their independent history.

Now that we have defined the structure of a pVCV matrix, we can return to the Brownian motion model of trait evolution to understand why the pVCV matrix is useful. As noted above, a Brownian motion model was the original model of trait evolution used to describe the expected level of nonindependence between two lineages. Brownian motion in a phylogenetic



	A	B	C	D	E
A	17	10	10	10	0
B	10	17	14	14	0
C	10	14	17	15	0
D	10	14	15	17	0
E	0	0	0	0	17

FIGURE 2.4. An example of how a phylogenetic variance-covariance (pVCV) matrix (right) relates to a phylogeny (left). Here, the species are letters and the numbers above the branches represent branch lengths. The diagonal elements of the pVCV are the root-to-tip distance. The off-diagonal elements represent shared evolutionary history (i.e., shared branch length).

context represents a drunkard's walk along a branch. The expected variance in where the drunkard ends their walk is proportional to the number of steps (i.e., the branch length walked). This brings us to the variance component of the pVCV matrix. The distance from the root to the tip of a tree is the distance a drunkard walks to a given tip (e.g., species). The expected variance for a trait is proportional to this value. Thus, we can see why the root-to-tip distance represents the expected variance in a trait under a Brownian motion model.

Next, we should imagine two drunkards starting to walk from the root of the phylogeny toward the tips, holding hands. Note that the drunkards are walking together randomly as a unit and are not pulling each other in opposite directions or averaging each other out or interacting in any way. Rather, they both step in the same random direction at the same time. At an internal bifurcating node in this tree, the drunkards drop hands and follow different branches going forward and become independent. Prior to this point they were walking in unison and, therefore, perfectly covarying. In other words, the amount of branch length that they shared indicates their expected trait covariance under a Brownian motion model of trait evolution. Thus, we can see why the off-diagonal elements of a pVCV matrix represent covariance. In sum, a larger off-diagonal element indicates a higher degree of expected trait covariation between the two tips being compared.

Given our understanding of how pVCV matrices are calculated and what they represent in a Brownian motion model context, we can discuss the two most widely used metrics of phylogenetic signal in the ecological (and evo-

lutionary) literature. The first seeks to quantify how well the observed trait data fit the pVCV from a given phylogeny. The second seeks to fit a pVCV to the data by transforming it where no transformation indicates that Brownian motion is the best fit. Thus, the metrics may appear to be two sides of the same coin, but they are calculated in very different ways and are not always strongly correlated.

The first metric we will discuss is often referred to as Blomberg's *K*, which was published over a decade ago by Blomberg and colleagues (Blomberg et al. 2003). The metric computes an observed and expected mean squared error in the trait data given the phylogeny, MSE_0, and *MSE*, respectively. We will use the original notation, where $\boldsymbol{V}$ represents the pVCV matrix. The MSE_0 can be calculated as

$$\mathrm{MSE}_0 = \frac{(\mathrm{X} - \hat{\mathrm{a}})'(\mathrm{X} - \hat{\mathrm{a}})}{\mathrm{n} - 1},$$

where *n* is the number of tips in the phylogeny, $\boldsymbol{X}$ is a vector of the trait values, and a is the phylogenetically corrected mean, which is equivalent to the estimated trait value at the root of the phylogeny (Garland et al. 1999). This is calculated as

$$\hat{\mathrm{a}} = \frac{\mathrm{v}^{-1}\mathrm{X}}{\Sigma\Sigma\mathrm{v}^{-1}}.$$

Next, the *MSE* is calculated as

$$\mathrm{MSE}_0 = \frac{(\mathrm{X} - \hat{\mathrm{a}})'\mathrm{v}^{-1}(\mathrm{X} - \hat{\mathrm{a}})}{\mathrm{n} - 1}.$$

The ratio can then be used as a measure of phylogenetic signal for a given phylogeny. However, as Blomberg et al. (2003) point out, this value is specific to a phylogeny and not comparable across studies. It is therefore standardized by a Brownian motion expectation to produce the value referred to as *K*:

$$\mathrm{K} = \frac{\mathrm{MSE}_0 \big/ \mathrm{MSE}}{\frac{1}{\mathrm{n} - 1}\ \mathrm{trV} - \frac{\mathrm{nn}}{\Sigma\Sigma\mathrm{v}^{-1}}}.$$

Thus, when a *K* value is equal to 1, the observed trait data are no different than that expected by a Brownian motion model trait evolution on the given tree. When *K* exceeds 1, the data have more phylogenetic signal than expected from Brownian motion on the given phylogeny, and when the *K* value is less than 1, the trait evolution is more labile than a Brownian motion expectation on the given phylogeny.

The second metric we will discuss is often referred to as Pagel's λ (Pagel 1999). The goal of this metric is to transform the pVCV matrix such that it optimally fits variation observed in the trait data where fit is estimated using

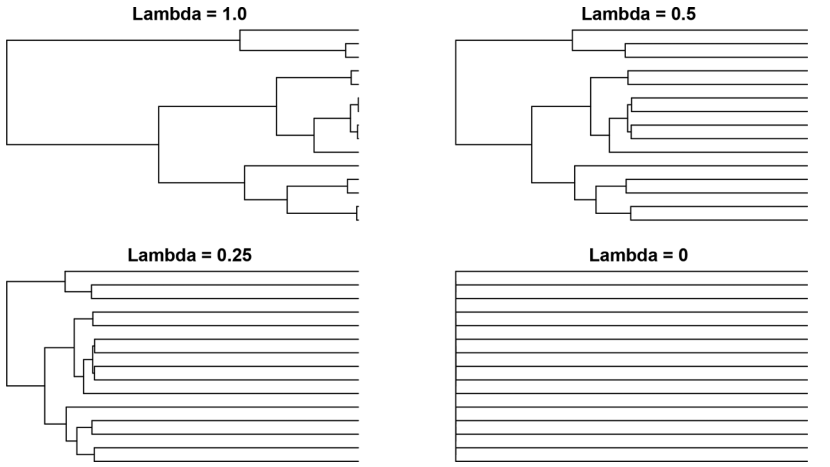


FIGURE 2.5. A phylogeny with four different λ transformations. A λ transformation multiplies the off-diagonal elements of a phylogenetic variance-covariance (pVCV) matrix, which reflect the amount of shared evolutionary history. A λ transformation less than 1 therefore reduces shared evolutionary time relative to independent evolution (tip branch lengths). The upper left is a λ transformation of 1, which retains the original structure. The upper right is a λ transformation of 0.5. The lower left is a λ transformation of 0.25. The lower right is a λ transformation of 0, which is no shared evolutionary history and all independent evolution. This is equivalent to all branches arising from a polytomous root node, which is also referred to as a "star phylogeny."

maximum likelihood. The λ represents the value used to multiply the off-diagonal elements of the pVCV (fig. 2.5). A λ of 1, therefore, indicates that the pVCV that best fits the data is the original matrix, which is constructed using a Brownian motion expectation. A λ transformation that is less than 1, therefore, reduces the amount of covariation expected between species, as the off-diagonal elements will decrease in value. If we were to plot a phylogeny that was λ transformed by a value less than 1, this would result in a phylogeny that would appear to have all internal nodes pushed basally, with the terminal nodes remaining in their original location. Thus, if the best fit λ transformation to a pVCV matrix (i.e., a phylogeny) given the data is less than 1, then the trait data are more labile than expected given a Brownian motion expectation. If the best fit λ transformation is greater than 1, then we may say that trait evolution has more signal than expected given a Brownian motion expectation.

The *K*, λ, and other metrics have been subjected to detailed scrutiny and comparisons in the literature (e.g., Revell et al. 2008; Harmon and Glor 2010; Münkemüller et al. 2012). As noted above, the metrics are not always correlated and simulation analyses have shown that they have different sensitivities to the number of tips in the phylogeny, the degree of signal in simulated data

sets, and unresolved nodes (i.e., soft polytomies) in the phylogeny. Generally speaking, λ performs best in such studies and is therefore recommended more often by those in the field (e.g., Münkemüller et al. 2012; Swenson and Worthy 2018). However, I am sure there are those that would argue against this recommendation, as comparative methods researchers are rarely uniform in their support of one approach over another.

Before I end this section, I would like to raise one peculiarity of the phylogenetic signal literature that I think merits discussion: metrics such as *K* and λ given values depicting phylogenetic signal relative to some value (1 for both of these metrics) expected under Brownian motion. However, randomization tests have also been traditionally used with these metrics in the literature, beginning, at least, with Blomberg et al. (2003). Specifically, the observed trait data are permuted across the tips of the phylogeny and random *K* or λ values are calculated during each permutation. This is done hundreds or thousands of times, until a null distribution of *K* or λ values is generated. The observed *K* or λ value is then placed in context of the null distribution to calculate its quantile and ultimately a *p* value. I am in favor of randomization tests in most cases, but more often than not, the results of this particular randomization raise conceptual and inferential problems. Specifically, a common result is an observed *K* or λ value much smaller than 1, but a *p* value that is below the 0.05 threshold. Thus, the observed distribution of traits is more evolutionarily labile than expected from Brownian motion, but the randomization tests suggest that they have "significant" phylogenetic signal. In other words, the randomization approach is more akin to asking whether there is more signal than expected from "white noise" (see Münkemüller et al. 2012), and not whether there is more phylogenetic signal than expected given a Brownian motion model. Thus, the researcher is then confronted with the problem of which results to choose or to believe. Does one say the trait has phylogenetic signal or not? What does it mean to have significant signal, but to be more labile than a random walk? This results in a literature that chooses to focus on the outcome (e.g., *K* vs. *p*) that best fits the story the researcher wants to tell, or highly convoluted and inconsistent language regarding whether a trait has signal or not. So, what is the ecologist to do? With the stipulation that the comparative methods literature is vast and rapidly expanding and I, therefore, could have missed it, I have not seen a serious discussion of this issue. This is in spite of the fact that the issue occurs frequently in the literature. If I were to offer my blanket recommendation, I would suggest that researchers focus on the *K* or λ value and only perform the permutation test if it exceeds 1. I say this for a couple of reasons. First, conceptually it makes no sense to me to say a trait has phylogenetic signal when it is also shown to have an

evolutionary history that is more labile than a random walk. Second, the permutation test essentially breaks apart all phylogenetic information while also randomizing the trait data. In doing so, it seems likely that Type I error rates are inadvertently inflated, which would explain the large number of "significant," but very low, K and λ values in the literature. I would suggest that a more appropriate null model, though, would be one that randomly evolves trait data on the phylogeny to calculate a distribution of K or λ values. This would likely lower Type I error rates and lead to a more conceptually and analytically consistent framework for quantifying whether a trait has significant phylogenetic signal. An alternative is to simply say there is more signal than expected from a white noise model, but less signal than expected from a Brownian motion model.

2.5. Searching for Phylogenetic Conservatism in Everything: Have We Gone Too Far or Asked the Wrong Questions?

Phylogenetic ecology has traveled from pointing out that phylogenetic nonindependence should be considered and likely exists to early objections to the incorporation of this nonindependence into study design. The availability of phylogenetic information and statistical code and the interest in phylogenetic community ecology has led to a place in time where quantifying phylogenetic signal in itself has become a goal (Kerkhoff et al. 2006; Gilbert and Webb 2007; Swenson and Enquist 2007; Ackerly 2009). Some now even argue that phylogenetic conservatism or signal is a unifying concept that underlies much more in ecological data sets than we had previously appreciated (Wiens et al. 2010).

The commonness of phylogenetic signal in ecological trait or niche data sets is not settled and likely depends substantially on the taxonomic scale of the sampling (Cavender-Bares et al. 2009) and how one defines phylogenetic signal conceptually and quantitatively (Blomberg and Garland 2002). It is hard not to appreciate the degree of phylogenetic signal in some ecological data sets or macroecological patterns, while in many other data sets there is clearly no signal to be found. Whether one is more common than the other is a potentially interesting question, but I think it is useful for the field of phylogenetic ecology to consider more seriously the research objective of measuring phylogenetic signal.

A common phrase in the phylogenetic ecology literature is that phylogenetic signal "explains" a pattern, whether that is species co-occurrence or the latitudinal species richness gradient. This wording implies an understanding of process, and to some may even mean the phylogeny itself explains

something. Neither of these are the case. First, a phylogeny can never explain something (Losos 2011). It is an attempt to infer the shared evolutionary history of a sampling of taxa. The phylogeny itself is not a process (e.g., competition). The phylogeny is the result of events and processes that have occurred. It is tempting to infer process from the structure of a topology, and this is a major research objective in the current macroevolutionary literature, but inferring a process from a phylogenetic pattern is fraught with problems (Losos 2011).

If we focus more narrowly on the quantification of phylogenetic signal as a pattern of traits distributed along the tips of a phylogeny that is no different from that expected if the traits evolved under Brownian motion, we can perhaps put a finer point on this argument. Brownian motion simulates a random walk or drift. Thus, if our traits have phylogenetic signal, does this mean we believe that selection played no role in producing the distribution of traits driving ecological interactions? This seems very unlikely. This also should lead us to question whether a process other than drift could lead to the same or a similar pattern of trait distributions on a phylogeny as that produced by drift. Revell et al. (2008) explored a similar thread of thought by quantifying whether the clade-wide stabilizing selection on a trait, a process that is decidedly not drift, could produce a pattern of phylogenetic signal. Their results demonstrated that this was indeed possible, underscoring the point that one should be careful to quickly infer the evolutionary processes underlying the present-day distribution of traits based on phylogenetic analyses alone. Thus, if we will struggle to infer evolutionary processes from studies simply quantifying phylogenetic signal, or don't even care to make such inferences in the first place, should this research objective be an objective? To answer this, we should take a closer look at the phylogenetic ecology literature and the types of phylogenetic signal studies that are produced.

As stated above, a great motivator for quantifying phylogenetic signal in the phylogenetic ecology literature was the growth of phylogenetic community ecology. This field originally and still often does rely on the assumption that there is phylogenetic signal in the traits or niche axes that influence community assembly, structure, and dynamics. This assumption has routinely been questioned conceptually and countered with data. A result of this was that quantifying phylogenetic signal began as a justification for the assumptions underpinning phylogenetic community ecology. Thus, in this rapidly growing literature, phylogenetic signal was not being measured in many or most cases for the purpose of inferring anything about evolution, but rather as a piece of evidence to defend an assumption (e.g., Swenson et al. 2007). I argue that this approach seriously sidetracked phylogenetic ecology for a

number of reasons. First, these studies were and are often conducted in small study areas with very diverse taxonomic samples. In other words, the taxonomic sampling is so small and so sparse (e.g., 25 angiosperm species from 12 families) that even attempting to make evolutionary inferences from a pattern of phylogenetic signal is pointless. However, I do note that this does not mean it is often attempted. Second, it introduced a pointlessly indirect analysis that I have called in the past the "phylogenetic middleman" (Swenson 2013). That is, a researcher might be interested in whether species with similar shade tolerances co-occur or not, and the processes that might govern that pattern. To conduct the analysis, they measure the relatedness of species as a way to measure similarity indirectly. Here, they are assuming that relatedness is correlated with similarity in shade tolerance. In the process of defending this assumption, the researcher may compile data on leaf traits and quantify phylogenetic signal in these data. The researcher may then find signal in the data and then infer a process governing co-occurrence from the pattern of relatedness. Or, the researcher could have totally omitted the phylogenetic component of this study and directly quantified leaf trait similarity to make more robust inferences. So, why bother, particularly if making an evolutionary inference is not possible or of interest? One might argue that since some traits have phylogenetic signal, others that cannot be measured likely do as well. However, this assumption is likely as tenuous as making the original assumption that relatedness indicates similarity, particularly if one has no a priori reason to believe the traits in question should evolve in a coordinated manner. In sum, there appears to be little reason to continue measuring phylogenetic signal in small local and taxonomically diverse samples of species when there is no possibility of making an evolutionary inference and other, more direct means of measuring similarity are possible.

A potentially more interesting approach to measuring phylogenetic signal as a research objective unto itself is achieved through the analysis of global-scale and taxonomically diverse data sets or the analysis of a well-sampled clade (e.g., Harmon et al. 2003; Moles et al. 2005; Swenson and Enquist 2007; Harmon et al. 2010). In such instances, taxonomic sampling is potentially dense enough to ask evolutionary questions. For example, how evolutionarily labile is vegetative trait X compared to reproductive trait Y? Is trait diversity higher than expected in lineages 1 and 5 and lower than expected in lineages 2, 3, and 4? However, as stated before, inferring processes from only these patterns will be difficult, and may in some cases only become slightly less treacherous with additional information. This is the nature of phylogenetic analyses, and I do not think this should prevent such analyses from taking place in the future. Indeed, I think we need more of them, and we are at

an exciting juncture in time where large enough data sets are becoming available for such endeavors. However, as phylogenetic ecology continues down this road of investigation, it would be useful to avoid the following traps.

First, if the work simply ends with the statement that there is phylogenetic signal in this trait or niche axis or not, then the work likely will have little utility. At minimum, it should include a demonstration of why that signal is important for understanding the ecological patterns of interest and/or additional independent information that should be used to help elucidate the processes that have produced the phylogenetic signal observed. One might also add that ahistorical processes should also be ruled out. This may seem to be a reasonable suggestion, but generally speaking, the patterns or interactions of interest have not been generated over the past few years (e.g., the latitudinal gradient in species richness) or are governed by evolved organismal traits.

Second, the phylogenetic ecology literature seems to be heavily biased toward one-sided tests. That is, researchers are frequently interested in knowing whether their data has phylogenetic signal. If it does, then it is interesting. However, just as interesting or more interesting are those cases of antisignal or convergence. Interestingly, historically, the opposite has been the case where researchers have sought to identify the presence of convergence in community structure and diversity across systems, but it seems the pendulum has swung completely in the opposite direction, to the point where a lack of signal or antisignal is not something meriting further discussion. This shouldn't be the case, and phylogenetic ecology would do well to pay as much attention to those cases where signal does not exist and to find the drivers of these patterns.

Finally, I would like to discuss some practical applications of measuring phylogenetic signal in large-scale and taxonomically well-sampled databases. Such applications may not be widely appreciated, but they are likely to become more widespread and important in the literature and should be encouraged moving forward. The first application I will describe comes from the tree ecology literature, where researchers are attempting to measure carbon stores and fluxes in forests. Tree ecologists and foresters frequently estimate the aboveground biomass of a tree via allometric equations and measurements of trunk diameter. However, these estimates can be heavily biased, based upon interspecific variation in canopy size, height, and the density of wood. Error propagation via the assumption of a constant wood density across species came to the attention of tree ecologists in the 2000s who were interested in estimating forest biomass across scales (Chave et al. 2004; Molto et al. 2013). However, wood density is a laborious trait to measure that

may have adverse influences on the health of the tree. Further, in diverse regions such as Amazonia, it seems unlikely that a wood density value for each species could be measured. Baker et al. (2004) proposed to solve this issue, basing their argument on a rough measure of phylogenetic signal in wood density data. Specifically, they performed a taxonomically nested partitioning of variance in the trait, finding that 45.6% of wood density was found between genera and 29% was found within genera. In other words, very little variation exists within genera, and it is therefore perhaps reasonable and more practical to use a congeners wood density value for a species that has no value or even the average of the known congeneric values. This approach has now been validated by other researchers as a way to reduce error propagation and is now widely used in the forest ecology literature.

A second practical application of phylogenetic signal in large databases comes from Gilbert et al. (2012). The fundamental questions asked by this team of researchers were how likely two species of plant were to share the same pest or pathogen and whether the answer to this was predictable based upon phylogenetic information. To address these questions, the team analyzed US Department of Agriculture data sources on pest and pathogen host ranges and cast this information in the context of the phylogenetic distance between two hosts. Gilbert et al. (2012) found that the probability of sharing a pest or pathogen between two host plant species declined approximately exponentially with the phylogenetic distance separating them. While this may be of general interest to plant ecologists, a clear practical application of the results is to estimate the probability that an invasive species or a species to be imported will carry a pest or pathogen that could jump to a host in the native flora or key agricultural crops. As we will discuss in chapter 8, using phylogenetic signal to make predictions for practical applications is becoming more feasible, with promising early results suggesting that this is a realm of phylogenetic signal analyses that should continue into the future.

The measurement of phylogenetic signal in data has gone from something rarely done in ecology to being frequently measured. Signal may be measured for the practical reason of identifying whether or not phylogenetic nonindependence must be considered in a researcher's statistical model. Increasingly, though, measuring signal has become an objective unto itself. Here, I have outlined the problems with this trajectory and where investigations into phylogenetic signal should or should not go in the future. In short, researchers should move away from measuring signal in local-scale samples and/or samples with poor taxonomic sampling and measuring signal as an investigative endpoint and toward coupling measures of phylogenetic signal in large and/or densely sampled data sets with additional sources of evidence to dem-

onstrate the evolutionary processes that may have given rise to the observed phylogenetic signal or how that phylogenetic signal changes our perspective on present-day ecological interactions.

2.6. A Very Brief, Basic, and Incomplete Overview of Phylogenetic Comparative Methods and Approaches

We now have a good grasp on the concepts of phylogenetic nonindependence, phylogenetic signal, and phylogenetic conservatism. As we have seen, the measurement of these things has increasingly been a research goal in and of itself. However, they serve as foundations for why and when phylogenetic comparative methods should be used in a study. In brief, if there is phylogenetic signal in the data, then a key statistical assumption, independent data, is violated and standard statistical tests are no longer valid (Felsenstein 1985). If there is no phylogenetic signal, then standard tests may be used with more confidence, but incorporating phylogenetic information may still be valuable (Harvey and Pagel 1991). Thus, the first steps in any comparative study should be to consider phylogenetic relatedness during the design of a study (Weber and Agrawal 2012), if possible, and to quantify phylogenetic signal in data prior to conducting additional statistical analyses. If signal is found, for better or worse, one must begin to wade through the comparative methods literature. This literature almost certainly must be one of the most daunting and tedious to read in ecology. It is vast, it is rapidly moving, it requires careful tree-thinking, and it is full of very strong opposing opinions emanating from very quantitatively astute experts. It would be foolhardy to attempt to comprehensively review this literature, much less to attempt to do it in one chapter, or worse, in a couple of pages in a chapter. However, I will venture to provide a very brief, basic, and incomplete discussion of phylogenetic comparative methods in the next few paragraphs. This is designed to serve as an entry point into the literature beyond the measurement of phylogenetic signal to gently get the novice ecologist on their way.

We will begin with a phylogenetically structured but phylogeny-free approach that has served as a viable way to design an experiment when there is no phylogenetic tree available—taxonomically paired comparisons. For example, imagine a study attempting to test whether a certain leaf trait changes across two habitats—closed- and open-canopy forest. One could design a study simply measuring the trait in the two habitats, but if the two habitats are composed of two distinct clades, then we have effectively no power to detect a significant shift in trait values with habitat. However, if we could design the experiment such that we studied a series of 10 genera where there

is one representative in each habitat, we could contrast the trait values of each of the congeneric pairs across the environments (e.g., a paired *t*-test) to provide a phylogenetically informed test of whether changes in trait values are significantly related to a change in the habitat (e.g., Swenson 2009b). Note that this design could also be used to correlate two continuous traits and need not be applied to only the shift in a single continuous trait given another categorical variable. Limitations of such experiments include the difficulty of implementing the experimental design due to few species and higher taxonomic levels in the system and clade-environment associations (i.e., phylogenetic signal). These studies also treat all pairs as having similar amounts of independent evolution, which is a flawed assumption. In other words, each congeneric pair is assumed to have a most recent common ancestor of the same age, but this is not possible. Thus, the expected amount of trait deviation between a pair given their time since divergence and Brownian motion is unknown and may bias the analyses.

A widely used alternative to the paired species design is Felsenstein's phylogenetically independent contrast (PIC) method (Felsenstein 1985). The method first estimates the trait value for all internal nodes in the phylogeny using the known trait values and, in most contemporary studies, branch length information. This is done for the two continuous trait values an investigator is interested in correlating. Next, for each internal node, a difference or contrast in the daughter node values is calculated for each trait. These contrast values are independent of one another, as they reflect trait evolution after the point of shared ancestry (i.e., terminal to their phylogenetic covariance or nonindependence). Given that they are independent, the contrasts can be used as data points in a standard correlation analysis. Recall that in a perfectly bifurcating tree, the number of internal nodes is one less than the number of species. In other words, one degree of freedom has been lost using this approach, but this is inconsequential in most modern analyses that use moderate- to large-size phylogenies.

The PIC method is a special case of a phylogenetic generalized least squares (pGLS) regression model (Martins and Hansen 1997; Garland and Ives 2000). The pGLS is now widely used in the literature and is simply a generalized least squares model with a phylogenetically informed error matrix. This error matrix is often based on Brownian motion and takes the form of a pVCV matrix. More advanced approaches use maximum likelihood to fit the pVCV to the trait data and use this transformed matrix as the error matrix in a pGLS. This offers extra flexibility and avoids the overly simplified (and therefore often criticized) Brownian motion model assumption. Finally, while we won't discuss it here, researchers have demonstrated how the pGLS

can be extended to generate phylogenetically informed analysis of variance and *t*-tests and how the pGLS framework could accommodate intraspecific trait variation (e.g., Revell 2012).

The final class of methods I will describe are somewhat controversial in the comparative methods literature. These are called phylogenetic eigenvector regression of phylogenetic eigenvector mapping approaches (Diniz-Filho et al. 1998, 2012b). The controversy with these methods surrounds two issues. First, these methods do not explicitly define a model of trait evolution. Second, they are prone to model overfitting and the selection of the eigenvectors to be used in the statistical model is not well defined (Rohlf 2001; Freckleton et al. 2002). Conceptually, the first issue is legitimate, but one may argue in response that claiming methodological supremacy due to a Brownian motion model of trait evolution being invoked is flimsy. The overfitting and eigenvector selection critiques were certainly valid early in the development of these methods, as it is, indeed, easy to overfit these models and eigenvector selection is a perennial issue. However, some of these methodological issues have been resolved, or at least the decisions have been clarified (Diniz-Filho et al. 2012a), such that I feel comfortable including a discussion of the methods presently. In brief, phylogenetic eigenvector methods use a phylogenetic distance matrix where diagonal elements are zero and off-diagonal elements are the sum of the branch lengths connecting two species. Thus, the distance matrix is similar to the pVCV in some respects, but it is distinct. The distance matrix is then used in a principal components (PC) analysis, with the number of resulting PC axes equal to the number of tips in the phylogeny minus one. Generally, the loadings on the first PC axis reflect the division of tips between the two lineages emanating from the most basal bifurcation in the phylogeny. The second PC axis reflects the next most basal major bifurcation, and so on. The resulting eigenvectors can be used as independent variables in a linear model, for example. However, the next question is which eigenvectors to select such that the model is not overfit. A variety of approaches have been tested, including broken stick selection, selection of only eigenvectors correlated with the dependent variable, forward selection of eigenvectors, and iteratively searching eigenvectors to maximally reduce phylogenetic autocorrelation in the model residuals until the autocorrelation is below a given threshold (e.g., Moran's $I < 0.05$). The autocorrelation method has been shown to perform the best (Diniz-Filho et al. 2012a), though it does have the disadvantage of having to set an arbitrary stopping threshold. Despite the controversy around phylogenetic eigenvector methods and how one actually should select eigenvectors, there is one aspect that I find particularly attractive. That is, the eigenvectors represent different depths and regions of the

phylogeny, which makes the approach more flexible. For example, if there is strong phylogenetic signal in one region of the phylogeny and not others, this approach has more potential to detect it than an approach that assumes or fits a model of trait evolution over the entire phylogeny. Thus, whether one is trying to simply account for phylogeny in their comparative analyses or use it to predict or model unknown trait values, it is more flexible than some alternatives and therefore may perform better.

2.7. Conclusions

I would like to end this section and chapter reiterating that I have attempted to provide a primer of concepts and methods from the comparative methods literature utilized in ecology. What I have presented is, by design, a brief and limited overview meant as an introduction for the novice. As one begins to consider their data and research questions in more depth with a phylogenetic framework in mind, no doubt they will need to consult the comparative methods literature to determine what alternative and new methods exist beyond the few I have discussed presently.

3

The Measurement of Phylogenetic Diversity

Biodiversity is now a foundational concept and term in biology (Magurran and McGill 2010). Biodiversity is a driver of new scientific enquiry, continued professional and amateur exploration, and environmental policy. The term "biodiversity" for many has been and still is roughly synonymous with the number of species in a space or time (i.e., alpha diversity). Ecologists have extended this framework to consider the number of species at larger spatial or temporal scales (i.e., gamma diversity) and the dissimilarity of samples taken at different places or times (i.e., beta diversity) (Anderson et al. 2011). These metrics may be weighted by factors such as the sampling effort or the relative dissimilarity in the number of individuals per species in the sample, but species remain a core component of the concept and calculation of biodiversity.

Biologists have been documenting and studying diversity long before it was termed "biodiversity." At times over the past centuries, biologists have worked with a much broader framework for conceptualizing and calculating biodiversity. The motivations for this broadening have been varied and oriented toward solving a specific pressing problem. In the past 10 years, however, ecologists and evolutionary biologists have installed a broad conceptual foundation for biodiversity science. Phylogenetic diversity has emerged as one of the key pillars supporting this broadened foundation (Tucker et al. 2017). The measurement of phylogenetic diversity seeks to weight the number of species in a sample by their shared evolutionary history (i.e., nonindependence). Thus, just as biologists have added information to their measures of species diversity by weighting the value by the commonness or rarity of species, they have also sought to add information regarding their shared evolutionary histories.

The measurement of diversity weighted by shared evolutionary history

has been present in ecology and conservation biology for a century. The measurement of phylogenetic diversity per se (i.e., a measure that incorporates a phylogenetic tree and not simply taxonomic ranks) began to be formalized in the 1990s. Conservation biologists led this formalization, with Daniel Faith playing a particularly important role (Faith 1992, 1996). They saw that phylogenetic nonindependence was not simply a statistical nuisance, and that it offered valuable information that can help refine our documentation, management, and conservation of biodiversity. From there, a revolution was born in conservation science. A decade later, this phylogenetic diversity revolution intertwined with a long-running interest in community ecology in quantifying the similarity of species as a means for understanding community assembly and species co-occurrence (Webb et al. 2002). This confluence has resulted in an enormous phylogenetic diversity literature that spans the applied and basic sciences, pushing a new generation of conservationists and ecologists to develop their understanding of phylogenetics (Tucker et al. 2017).

This chapter aims to provide some historical background, beginning with the development of phylogenetic diversity metrics in the 1990s and how the concepts and metrics from this literature have impacted community ecology and macroecology and vice versa. In acknowledging up front that the phylogenetic diversity literature is large at this point in time, I have sought to keep these historical sections brief, highlighting what I believe are key developments rather than providing an exhaustive overview of the entire literature. This chapter, more importantly, covers the basics of measuring phylogenetic diversity using widely used and tested metrics, comparing and contrasting their similarities conceptually and quantitatively. I end with some commentary on choosing the ever-elusive "best" phylogenetic diversity metric and ecology and evolutionary biology's broadened foundation for conceptualizing and measuring biodiversity.

3.1. Faith, Vane-Wright, and Setting Conservation Priorities

The use of phylogenetic trees in ecology began in the early 1990s. I note later in this chapter and in other chapters that ecologists were using measures of relatedness in their studies in the early 1900s, but it was not until the 1990s that phylogenetic topologies began to be explicitly considered. The original stimulus for including topological information in ecological studies was to provide alternative measures of biodiversity that could be utilized to set conservation priorities. Specifically, when difficult decisions must be made, how should a conservationist prioritize species? Measures of species richness do not provide information useful for prioritization, as they effectively treat all

species as equal. The questions, therefore, are how we differentiate species and how we value this differentiation.

The first attempt to use phylogenetic topologies to address these questions was made by Vane-Wright et al. (1991). They proposed a measure that is known as taxonomic distinctiveness. The goal of this metric is to assign a value to each individual species in a phylogeny that describes how evolutionarily distinct it is from the other species in a phylogeny. Thus, if one is given a phylogeny of the species in a region and asked to prioritize the conservation of a species, then this measure may be used to indicate priority based on distinctiveness. The distinctiveness of each species was originally measured using just the topological information in a phylogeny. For each species, one over the number of node splits leading to a species from the root of the phylogeny is calculated. Thus, species with few internal nodes (e.g., a mono-specific lineage emanating from the root node) will have the highest distinctiveness.

There are some key advantages of the Vane-Wright metric. First, it does not require phylogenetic branch lengths. This means it could be implemented on crude phylogenies or even utilized based on taxonomic ranks, and therefore could be utilized widely, particularly by conservationists that do not frequently have phylogenies with branch lengths containing all species in the system of interest. Second, it assigns a single value to each species, which means individual species can be prioritized. There are several downsides, however, that have likely prevented the widespread use of this metric. One issue is the focus on counting nodes, which is problematic given the potential for different rates of lumping and splitting by systematists working on different lineages and because, in a phylogeny containing only species from a given geographic region, "real" nodes may be missing and therefore bias the metric. Another issue is that a conservationist may be more interested in prioritizing assemblages and not species, and the lack of clarity regarding how the Vane-Wright metric might be summed to represent an assemblage reduces the adoption of the metric. It should be noted that both of these issues have been largely mitigated by the development of evolutionary distinctiveness measures that utilize branch lengths. Finally, even if one is interested in species-level distinctiveness, the Vane-Wright metric calculates distinctiveness of species given a phylogeny, and the level of distinctiveness is not dynamic. That is, if there are two species that are derived from a single long branch emanating from a root node, it might make sense to begin by prioritizing one, but would the species with the second-highest priority be the most closely related species to the first? Conceptually, this does not make sense—at least to me. Rather, one would want to calculate the most

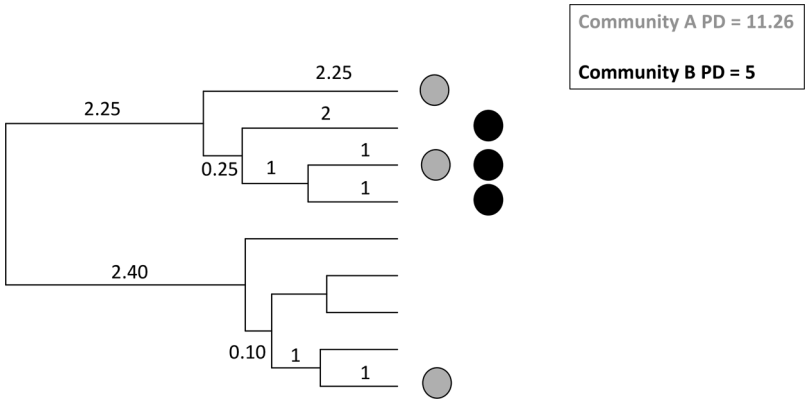


FIGURE 3.1. An example of Faith's phylogenetic diversity (PD) calculation. The PD is calculated as the sum of all branch lengths subtending the species in a community. In this example, there are two communities (A and B) that both have a species richness of 3. Community A, however, is composed of a more phylogenetically diverse set of species.

distinctive species *given* what is already in the sample. The original metric does not clearly consider this issue, and to some degree it is not well considered in most metrics still utilized in conservation today.

The second attempt to develop a measure of biodiversity that incorporates information regarding the evolutionary history of species that can be used for setting conservation priorities was made by Faith (1992). Faith's phylogenetic diversity metric, now widely called PD, was designed to quantify the diversity of a sample of species and not to provide a species-level metric. The goal of the metric is to sum the evolutionary history represented in a sample (fig. 3.1). Implementations of the metric that do not utilize branch lengths can simply sum up the internal nodes from a phylogeny that connect all species in the sample. Such a node-counting procedure has the same pitfalls as other node-based metrics, like the Vane-Wright metric just described. However, the Faith metric is now generally quantified by summing all the branch lengths connecting the species in the sample. This measure was widely adapted in the conservation literature, and it still remains dominant, to the point that the Vane-Wright metric is frequently forgotten about in discussions of phylogenetic diversity. As I will discuss below, the Faith metric also serves as the foundation from which many tree-based metrics of phylogenetic alpha and beta diversity have been derived. Despite the success of the Faith metric in conservation biology, it has been less popular in the community ecology literature. Rather, the rapid increase in measures of phylogenetic diversity in community ecology was associated with other metrics. I will briefly describe this history and the potential reasons for this outcome in the next section.

3.2. Community Ecology's Adoption of Phylogenetic Diversity from Conservation Biology

Taxonomic ratios (genus : species, family : genus, etc.) calculated from species lists were used in community ecology until the late 1990s and early 2000s (e.g., Enquist et al. 2002), until metrics utilizing phylogenetic trees began to become widely utilized. Interestingly, the metrics of phylogenetic diversity that became popularized during this transition did not include the Vane-Wright and Faith metrics. Rather, the metrics implemented were what I term "distance-based metrics." These metrics summarize a matrix of phylogenetic distances based upon nodal distances or branch lengths.

The early adoption of distance-based metrics in phylogenetic community ecology as it transitioned from taxonomic ratios to metrics based on phylogenetic trees is not as surprising as it may seem. The first reason for this is that a series of functional diversity metrics had been developed in community ecology prior to this time that focused on quantifying the trait similarity of species in communities using univariate or multivariate distances between species. For example, the pairwise distance between species in trait space had become popularized in trait-based community ecology, and nearest neighbor distances in trait space had been of interest to community ecologists since at least MacArthur and Levins (1967). Thus, the tools developed for and familiarity with distance-based measures likely led early community phylogenetics researchers to simply transform a phylogeny into a distance matrix rather than utilize the tree-based methods of Vane-Wright and Faith that sum branch lengths.

Another contributing factor to the use of distance- or dissimilarity-based measures of phylogenetic diversity in community ecology over tree-based measures was likely the tradition of thinking more about diversity rather than shared history. These are, of course, two sides of the same coin, but the amount of shared evolutionary history has clear conceptual foundations in the comparative methods literature, whereas dissimilarity is a more familiar concept to ecologists. This is not to say that early promoters of distance-based measures of phylogenetic diversity in community ecology (e.g., Webb 2000) were unfamiliar with comparative methods or tree-thinking. Rather, the research community that was reading their research was more prone to feeling comfortable with and therefore using dissimilarity metrics.

Currently, the ecological literature has strong representation of both distance- and tree-based methods of phylogenetic diversity (Swenson 2014a). This is due to a broader recognition of Faith's PD measure, increasing comfort with comparative methods and tree-thinking, the continued contribution of comparative methods researchers to the ecological literature, and computer

code that can calculate a wide variety of metrics. Thus, a researcher venturing into the world of phylogenetic diversity must confront the question not only of whether it matters if one should use a distance- or tree-based measure, but also which one of the many metrics to utilize for a given study. In addressing these questions, it is best to start with a conceptual and quantitative description of the main tree- and distance-based measures one might encounter in the literature. I will seek to describe these measures in the next section, with the admission that there are likely many more that are worthy of discussion.

3.3. Measures of Phylogenetic Diversity: Tree-Based Metrics

The first phylogenetic diversity metrics that actually used a phylogenetic tree were those developed by Vane-Wright et al. (1991) and Faith (1992). Cladograms were used by Vane-Wright et al. (1991) to present possible approaches for introducing phylogenetic information into the measurement of biodiversity. Faith (1992) explicitly considered the lengths of branches in the phylogeny, which is why his metric is often considered to be the first true phylogenetic diversity metric. Both of these metrics and their derivatives are what I consider to be tree-based metrics. I call them this because they consider the shared topology *and* the phylogenetic distance between species. I also refer to them as tree-based metrics because operationally their calculation typically requires a phylogenetic tree file, while other measures can simply utilize a matrix representing the distances between species without knowing the original topology of the phylogenetic tree itself. At present, tree-based metrics of phylogenetic diversity are more commonly employed in conservation biology and microbial ecology, and to a lesser extent in the community ecology of macro-organisms. As I explained above and will explain again in section 3.3, some of this can be explained by historical legacies regarding who developed the metric, but in many instances this lack of overlap in metrics utilized is for good reason. Here, I will present the most commonly utilized tree-based metrics for calculating alpha and beta phylogenetic diversity. I do note that new or "novel" metrics of phylogenetic diversity routinely appear in the contemporary literature. Many of these are redundant or minor derivatives, while some are truly novel and capture important information not easily extracted with existing metrics. Thus, the reader is advised that the following is meant to be an entry point into the phylogenetic diversity metric literature that highlights the most commonly used approaches.

The first measure I will describe is Faith's PD index. This classic metric is probably still the most widely used measure in conservation biology. The metric begins with a phylogeny of all possible species and prunes it to only

include those species in the assemblage being studied. From this phylogeny only containing the species in the sample, the branch lengths (l) are summed:

$$\text{Faith} = \bullet \sum_{i}^{n} l_i,$$

where i indexes the individual branches in the phylogeny. The pruning of a larger phylogeny to a smaller one only containing the species in a sample is not how the metric is typically explained, but it is how it is typically programmed. The way it is generally explained is the sum of the branch lengths connecting all species in a sample on a given phylogeny. It is worth noting at this point that Faith's PD must increase as the number of species in a sample increases (fig. 3.2). Thus, some may view it as biased or nonindependent of species richness (e.g., Helmus et al. 2007). While this is true, the bias may be useful and desired in many cases. For example, a conservationist may want to reflect the dual importance of species richness and phylogenetic diversity such that adding more species is always "good," but from a given level of phylogenetic diversity it could increase to varying degrees when a species is added, given its relatedness to the species already in the sample.

In some iterations of Faith's PD, it is scaled to the total tree length (i.e., the sum of all branch lengths in a larger tree). This standardization of the metric may be useful in some instances, but it is largely no longer utilized. One reason for this is that researchers now frequently report this measure in millions of

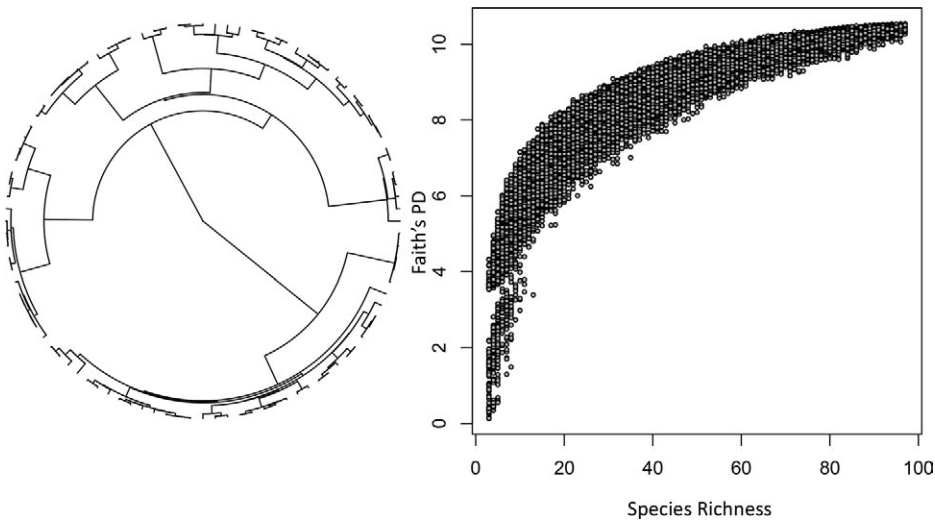


FIGURE 3.2. The relationship between species richness and Faith's phylogenetic diversity metric, where samples of species were randomly compiled from the phylogeny on the left. For some, this correlation between these measures is problematic, but for others it is useful to have an additive metric of phylogenetic diversity.

years, which could be a standardized measure across systems. However, this is not quite true, as the same node may have quite different ages across the phylogenies used in different studies. This problem would still lurk in studies that divide Faith's PD by the total branch length in a phylogeny and, worse, dividing by the total branch length in a phylogeny is biased by the size of the phylogeny a researcher uses in his or her study and therefore cannot be as easily compared.

An oft-mentioned downside of Faith's PD metric is that it does not consider the abundances of species in the sample. This omission is understandable, given that the metric was originally designed for conservation purposes where the diversity of large areas, where presumably species abundance could not be estimated, was the focus. There is, however, a version of Faith's original metric that is weighted by abundance (Barker 2002). It is calculated as

$$\text{Weighted.Faith} = n \times \frac{\sum_i^n l_i \overline{A_1}}{\sum_i^n \overline{A_1}},$$

where Ai is the average abundance of all terminal nodes, in most cases species, descendent from branch *i*. Thus, long branches subtending species with high average abundance disproportionately increase the diversity. Similarly, the addition of a new species maximizes diversity if it is distantly related and common more than if it is equally distantly related and rare. This metric is far less commonly used, as compared to Faith's original metric, and it is almost entirely absent from the community ecology literature, but it is an important development and dispels the widespread notion that there is no abundance-weighted version of Faith's metric.

As mentioned above, the original Vane-Wright et al. (1991) metric of taxonomic distinctiveness has been improved to include branch length information (Redding and Mooers 2006). This modified metric is called evolutionary distinctiveness, and it is typically measured using the "equal splits" method as

$$ES(T, i) = \sum_{e \in q(T,i,r)} \lambda_e \prod_{v \in a(T,i,e)} \frac{1}{\deg_{out}(v)},$$

where the species *i* is in the tree *T* and the set *q*(*T*, *i*, and *r*) defines the internal node splits between the species and the root *r*. The value of $deg_{out}(v)$ describes the original taxonomic distinctiveness (i.e., a value of 2 per node split), and λe describes the length of a branch, *e*, that subtends the split. Thus, in plainer terms, the distinctiveness is enhanced if there are long branches leading to the species of interest. This metric is utilized with some frequency in the conservation literature, reflecting the value still placed on obtaining a value that can be utilized to prioritize individual species. However, this metric is not commonly utilized in the community ecology literature.

Tree-based measures of phylogenetic alpha diversity have existed for decades, but only over the past decade have tree-based phylogenetic beta diversity measures been developed. The first measure that was developed sought to quantify the uniqueness of communities given the relatedness of all species in the two communities. In other words, it is a dissimilarity measure where if there is a higher amount of uniqueness (i.e., beta diversity), the metric is higher. This metric is called *UniFrac*, which is short for unique fraction (Lozupone and Knight 2005). It can be defined as

$$\text{UniFrac}_{A,B} = \frac{\text{PD}_{A\cup B} - \text{PD}_{A\cap B}}{\text{PD}_{A\cup B}},$$

where the value $\text{PD}_{A\cup B}$ represents the phylogenetic diversity of the species in communities A and B combined, as measured with Faith's PD index. The value of $\text{PD}_{A\cap B}$ is the phylogenetic diversity of the species shared between communities A and B, again using Faith's metric. Note that this metric is essentially the phylogenetic analogue of a Jaccard dissimilarity. Further, it does not utilize the abundances of species, and therefore, additional information about the dissimilarity of assemblages is missing.

An abundance-weighted measure of the *UniFrac* method has been proposed by Lozupone et al. (2007). This new metric is calculated by dividing the raw *UniFrac* value (U) by a scaling factor based on species abundances (D). To start, we can rewrite the raw *UniFrac* calculation as

$$u = \sum_i^n b_i \times \left| \frac{A_i}{A_T} - \frac{B_i}{B_T} \right|,$$

where b_i is the length of the individual branch i, with a total of n branches in the given phylogeny. Recall that the phylogeny must contain all species from the two assemblages being compared and no other species. For each individual b_i, the value is multiplied by the absolute value of the difference between the abundance of the species subtended by branch i in community A (A_i), divided by the total abundance in community A (A_T), and the abundance of the species subtended by branch i in community B (B_i), divided by the total abundance in community B (B_T).

Next, the scaling factor (D) is calculated as

$$D = \sum_j^n d_j \times \frac{A_j}{A_T} + \frac{B_j}{B_T},$$

where d_j is the distance from the root to the branch tip for species j of n total species. If the phylogeny is ultrametric, then the value for d_j will be the same for all species. The abundances of species j in community A (A_j)

and community B (B_j) are divided by the total abundance of all species in community A (A_T) and B (B_T). Ultimately, the abundance-weighted *UniFrac* measure is equal to U/D. A problem with this metric is that if abundances are turned into binary presence-absence data, the new metric is not equivalent to the original *UniFrac* metric. This inconsistency, and the proposed solutions to it, are perhaps the main reasons why the abundance-weighted *UniFrac* measure is infrequently utilized in the literature and almost completely absent from the literature outside microbial ecology.

There is a second tree-based measure of phylogenetic beta diversity frequently encountered in the literature. Curiously, the measure was originally proposed as being a "new" measure of phylogenetic beta diversity, with qualities that make it preferable to other commonly used measures such as *UniFrac*. This metric, called *PhyloSor*, was presented by Bryant et al. (2008), and it is a similarity measure derived that is a phylogenetic twist on Sorenson's index. It can be calculated as

$$\text{PhyloSor} = 2 \times \frac{\text{BL}_{\text{K}_1\text{K}_2}}{\left(\text{BL}_{\text{K}_1} + \text{BL}_{\text{K}_2}\right)},$$

where BLk1k2 is the phylogenetic diversity, calculated using Faith's metric, of the species shared between two communities. The BLk1 and BLk2 values are the Faith's metric values for the two individual communities. Either by simply looking at the equations for *PhyloSor* and *UniFrac* or by calculating them on the same series of data sets, one can quickly find that they are negatively related and monotonic. In other words, the ranks of beta diversities between a set of communities are identical (fig. 3.3). There is a slight curvature in the relationship between the two, but I have yet to determine a valid reason why, based upon important ecological processes, this makes one preferred over the other. Similar to the Faith metric, these phylogenetic metrics are strongly related to species metrics. Specifically, they are strongly correlated with Jaccard's dissimilarity index. This may be preferred, but if one is interested in determining if the phylogenetic information tells us anything beyond what we can learn from species lists, then a null model may be required (Swenson 2011b).

The metrics presented in this section explicitly consider phylogenetic topologies. Further, they cannot be calculated easily using a phylogenetic distance matrix. While their use is common in the conservation literature and to some extent the microbial ecology literature, they are less utilized in other fields of ecology. In the next section, I will discuss the distance-based metrics of phylogenetic diversity that are more common in the ecology literature.

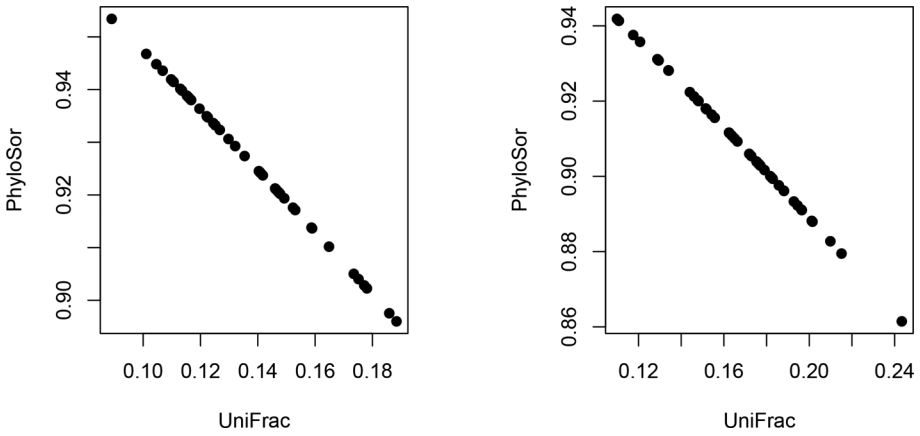


FIGURE 3.3. The correlation between the phylogenetic beta diversity metrics UniFrac and PhyloSor, generated using a phylogeny of 100 species and randomly assembled communities. The PhyloSor metric was purported as being a new metric when published (Bryant et al. 2008), but as we can see, it is essentially the inverse of UniFrac. This highlights a common issue in the literature, where new or novel metrics published are often not vetted carefully or compared to other existing metrics, thereby bloating and confusing the literature.

3.4. Measures of Phylogenetic Diversity: Distance-Based Metrics

The next class of phylogenetic diversity metrics we will discuss are what I call distance-based metrics. I call them this because all utilize a distance matrix as a centerpiece. The metrics are almost all adapted from the functional diversity literature and have been utilized in other contexts for decades prior to the phylogenetic community ecology explosion. The phylogenetic distance matrix ($\delta i,j$) that we will discuss, in almost every case, has zero in the diagonal to reflect zero distance between conspecifics, and the off-diagonal elements reflect the phylogenetic branch lengths separating two heterospecific species, *i* and *j*.

There are two general classes of distance-based phylogenetic diversity metrics—pairwise metrics and nearest neighbor metrics (Swenson 2011b, 2014a; fig. 3.4). Pairwise metrics are designed to quantify the overall dispersion or dissimilarity between species within a community or between communities. Traditionally, these metrics are intended to give an overall measure of diversity, but also to quantify whether the abiotic environment constrains the diversity in a sample. Nearest neighbor metrics, on the other hand, are typically used to indicate the strength of biotic interactions, with competition often being the interaction of interest. Thus, it has been frequently used in the context of limiting similarity and as a complementary metric to pairwise

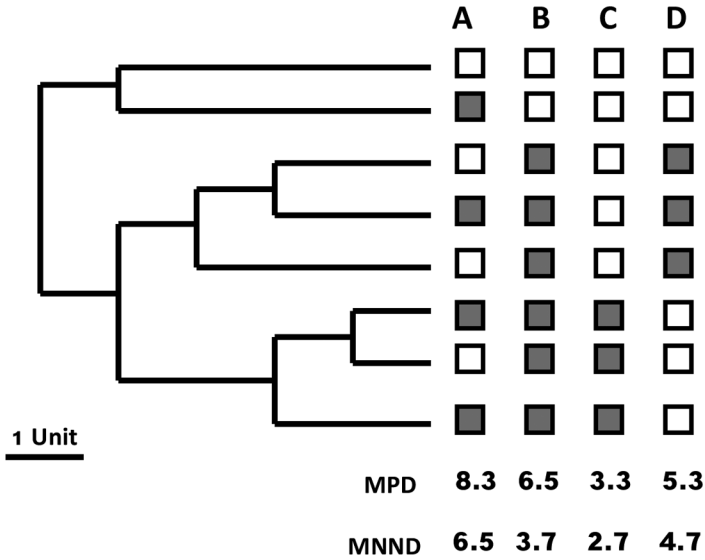


FIGURE 3.4. A simple example of how four communities may vary in their pairwise measure of phylogenetic diversity (MPD) and their nearest neighbor measure (MNND). Pairwise and nearest neighbor metrics are the two main classes of distance-based phylogenetic diversity metrics.

metrics. We will begin with discussing major pairwise metrics and then discuss nearest neighbor metrics.

The first metric we will discuss was and likely still is one of the two most widely used metrics of phylogenetic diversity in community ecology—the mean pairwise distance (*mpd*) metric. The metric had been used to measure functional diversity for the purposes of inferring community assembly mechanisms and was translated to phylogenetic community ecology by Cam Webb in 2000 (Webb 2000). The original formulation by Webb (2000) used node distances instead of branch lengths, but quickly *mpd* became calculated only using branch length information. The *mpd* for a community can be calculated as

$$\text{mpd} = \frac{\sum_i^n \sum_j^n \delta_{i,j}}{n}, \text{where } i \neq j,$$

where *n* is equal to the number of species in the community. Large *mpd* values are often considered evidence of overdispersion, and lower values indicate underdispersion or clustering. Most commonly, ecologists consider underdispersion to be evidence of a stronger environmental constraint on community membership. In the case of phylogenetic community ecology, this inference is made using the assumption that closely related species are functionally similar. In the next chapter, I will discuss how tenuous this assumption can be in ecology and evolutionary biology. There is also sub-

stantial controversy about whether underdispersion truly indicates the importance of the abiotic environment, with many suggesting it indicates the importance of competitive dominance of a group of similar phenotypes over a group of dissimilar phenotypes (Mayfield and Levine 2010). However, it is logical to infer that a strong abiotic constraint would promote the competitive dominance of a group of similar species. Thus, inferences derived from patterns of underdispersion from pairwise metrics likely should always invoke the importance of a strong abiotic constraint that selects a group of superior competitors.

Another important aspect of pairwise metrics, including *mpd*, is that they are generally not correlated with species richness. This is not the case for tree-based methods or nearest neighbor methods. Thus, many will state that they prefer pairwise metrics due to their independence from species richness. This viewpoint, however, is not quite correct and misses some important nuances. It is true that pairwise metrics are not correlated with species richness in random data sets. If they are correlated in real data sets, it might be informative and not cause for immediate concern. However, the range of possible values decreases with species richness. That is, the expected variance in metrics like *mpd* systematically decreases with species richness. Thus, *mpd* and other pairwise metric values are not easily compared in their raw form, as an exceptionally high value in a community with a species richness of 110 may be very unexceptional in a community with five species. Thus, a null model is often necessary to standardize values such that they can be compared across samples with very different numbers of species. Finally, the lack of a correlation between species richness and pairwise metrics may mean that they may be preferred or not, often vehemently so, by a given conservation biologist. That is, if a conservation decision is based solely on a metric like *mpd*, one may choose to conserve an area with five species over one with 110, which may result in a phylogenetically diverse and very species-poor conservation effort. Thus, care is needed when inferring mechanisms from, making decisions based upon, and comparing different levels of *mpd* values and other pairwise metric values.

The *mpd* of a community has been adjusted to incorporate species abundances (*mpd.a*) in order to consider the evenness of abundances across the phylogeny. This metric may be calculated as

$$\text{mpd. a} = \frac{\sum_i^n \sum_j^n \delta_{i,j} f_i f_j}{\sum_i^n \sum_j^n f_i f_j}, \text{where } i \neq j,$$

where f_i and f_j are the abundances or frequencies of species i and j, respectively. When abundance is evenly distributed across a phylogeny (i.e., low

phylogenetic signal in abundance), the *mpd.a* and *mpd* metrics will be strongly correlated. However, when abundance is clustered in a few clades, particularly in very distinct clades, the *mpd.a* and *mpd* values may have a much weaker correlation. Thus, if one is comparing the metrics and finds a weak correlation or no correlation, this should indicate to the researcher that a single clade likely dominates the assemblage. A practical way in which this might be informative is if the *mpd* value is high, indicating overdispersion, but the *mpd.a* value is exceptionally low. This would indicate that while many distantly related species co-occur, in reality, the community is largely full of closely related species. It is important for the user to realize that there is no right metric, and that comparisons of metrics, like the example I just provided, can be useful for gaining further insights into the structure of the community being studied.

The *mpd.a* metric appears very similar to another biodiversity metric often referred to as Rao's quadratic entropy (Rao 1982). Rao published a series of metrics for alpha and beta diversity, but his core alpha diversity metric can be written as

$$\text{Rao's } D_{\text{alpha}} = \frac{\sum_i^n \sum_j^n \delta_{ij} f_i f_j}{\sum_i^n \sum_j^n f_i f_j}$$

It is clear that this metric is highly similar to *mpd.a.* The key difference in Rao's metric is that it allows in the calculation the diagonal of the distance matrix. In plain language, it includes zeros in the summation, to reflect many or few conspecific individuals. In other words, if there are many conspecific individuals, then there will be many zeros in the summation in the numerator and give a lower value than one would get from *mpd.a.* There are some that believe this fundamental difference between Rao's D_{alpha} and *mpd.a* is very important and important biological insights can be gleaned by comparing them. I do concur that when communities are sufficiently species poor and abundances are highly skewed toward one to a few species dominating a community, the metrics will be very different and therefore inferences made by the ecologist may be very different. However, as communities or study regions increase in size, the diagonal elements increase linearly while the off-diagonal elements increase exponentially. Further, as communities become more diverse, it is less and less likely that only a few species comprise most of the abundance distribution. Thus, in diverse communities, the differences between the two metrics will be less noticeable, the metrics will become essentially monotonic, and the conceptual or philosophical arguments regarding why one is "better" become academic and not operationally important (fig. 3.5).

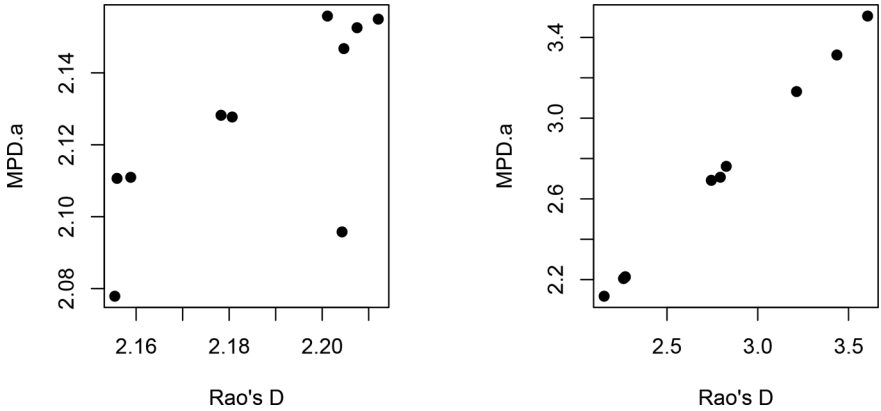


FIGURE 3.5. The correlation between an abundance-weighted mean pairwise distance measure (*mpd.a*) and Rao's measure of diversity (Rao 1982). On the left are randomly assembled communities of 10 species, and on the right are randomly assembled communities with 50 species. The communities were generated by sampling from the same phylogeny. Thus, at low species richness levels, the two metrics are correlated, but in some cases they diverge, and at high species richness levels, they are always strongly related and effectively redundant.

A subtle modification of the Rao D_{alpha} metric was introduced into the community phylogenetics literature by Hardy and Senterre (2007) and can be calculated as

$$D_k = \sum_i^n \sum_j^n \delta_{i,j} f_{ik} f_{jk},$$

where *k* represents the community identity. In this instance, there is only one community, as it is an alpha diversity metric, but Hardy and Senterre (2007) also discuss community dissimilarity in their work, making this notation necessary. We can see that this is almost identical to Rao's metric. It is unclear to me whether Hardy and Senterre (2007) realized this convergence. They were motivated to produce this metric, as it was essentially a phylogenetic analogue to the F_{ST} metric in population genetics. As Hardy is a population geneticist, it is not surprising to see this connection being made in his work. Like the Rao metric, this metric is strongly related to the *mpd.a* metric, also with the exception that it includes the diagonal elements in the distance matrix. Also, it is monotonic with Rao and may be used interchangeably from my perspective, though Hardy and Senterre's metric may be more easily translated into a diversity-partitioning framework.

A final series of pairwise phylogenetic alpha diversity metrics that we will discuss come from the work of Helmus et al. (2007). This collection of metrics is interesting for several reasons. First, the "distance matrix" being used in this series of metrics is not like the distance matrix we have discussed up to

this point. Specifically, the matrix being utilized is a phylogenetic variance-covariance matrix (Martins and Hanson 1997) like that used in much of the phylogenetic comparative methods literature. In a phylogenetic variance-covariance matrix, the diagonal elements reflect the distances from the root to the tip for a given species. These values will be identical across species if the phylogeny is ultrametric. The off-diagonal elements in this case do *not* reflect distances between species. Rather, they reflect the amount of branch length shared between two species; in other words, how much evolutionary time they have shared. The authors preferred this conceptual foundation, as it more clearly aligns with traditional comparative methods and models of trait evolution. A second interesting aspect is that, despite this different conceptual foundation, the core metric called phylogenetic species variability (*PSV*) is monotonic with metrics that existed in the literature at the time of publication (e.g., *mpd*). The equation for *PSV* can be simplified as

$$\mathrm{PSV} = 1/\overline{c},$$

where c is the average of the off-diagonal elements from a variance-covariance matrix composed of only the species in the community of interest. We can see why this is strongly related to *mpd*, as the off-diagonal elements of a phylogenetic distance matrix are distances between species and the off-diagonals of variance-covariance matrices are shared branch length. Thus, the differences between the two are two times the time since the most recent common ancestor between two species in chronograms or two times the branch lengths since the most recent common ancestor in ultrametric phylogenies not scaled to time. The strong relationship between *PSV* and *mpd* weakens when nonultrametric phylogenies are used, but such phylogenies are not commonly used in community ecology (fig. 3.6).

Aside from differences in the conceptual formulation underlying the *PSV* metric, the authors argued that it was valuable in that it was not correlated with species richness, as is the case with *mpd*. However, just like *mpd*, the expected variance in *PSV* decreases with species richness and it is, therefore, not a completely bias-free metric that can be directly compared across communities with very different species richness values.

In recognition that conservation biologists might want to combine a phylogenetic metric that is uncorrelated with species richness with species richness to have a composite measure of biodiversity, Helmus et al. (2007) next presented what they called the phylogenetic species richness (*PSR*) metric. The *PSR* is calculated as

$$\mathrm{PSR} = \mathrm{n} \times \mathrm{PSV},$$

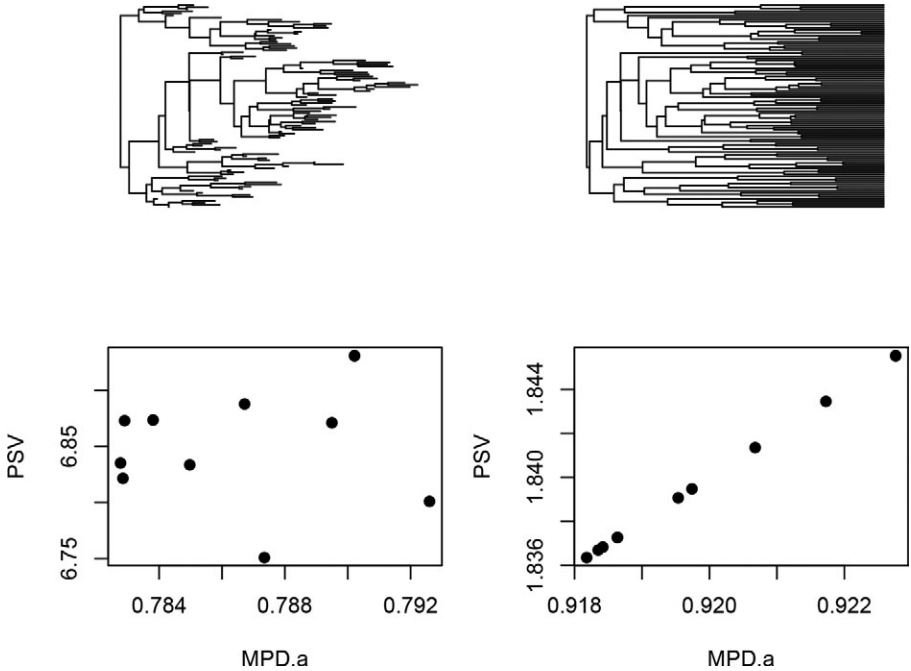


FIGURE 3.6. The relationship between abundance-weighted mean pairwise distance (*mpd.a*) and the PSV metric of Helmus et al. (2007). Note that when the phylogeny is ultrametric (right), the two metrics are perfectly correlated with PSV being double *mpd.a*. When the phylogeny is not ultrametric (left), the two metrics are not correlated.

where n is the number of species in the community. The inclusion of species richness in the calculation, of course, makes *PSR* strongly correlated with species richness and therefore may be a metric of more interest to conservation biologists.

The above certainly do not represent all pairwise metrics of phylogenetic diversity, but they do represent the core metrics from which subtle modifications have been made. While those modifications may be important in some instances, by and large, the additional metrics not covered will be strongly correlated with those described above. Therefore, we will now transition to pairwise phylogenetic beta diversity metrics. The first is a simple pairwise distance between all species in two plots not weighted by abundance (D_{pw}), and it can be written as

$$D_{pw} = \frac{\sum_i^{nk_1} \sum_j^{nk_2} \delta_{ij}}{nk_1 \times nk_2}$$

where the species richness of community 1, k_1, is nk_1 and the species richness of community 2, k_2, is nk_2. Note that in this instance, if a species is in both

communities, it is included in the calculation. This measure is generally used as an overall measure of phylogenetic similarity, but it is not strongly correlated with traditional measures of species beta diversity such as Jaccard and not correlated with *UniFrac* or *PhyloSor* (Swenson 2011b).

The *Dpw* metric has been modified to include species abundances, and it can be written as

$$D_{pw}' = \sum_i^{nk_1} \sum_j^{nk_2} \delta_{ij} f_i f_j.$$

This metric is essentially identical with a generalized beta diversity metric developed by Rao (1982), which is written as

$$\text{Rao's } D_{beta} = \sum_i \sum_j \delta_{ij} f_{ik_2} f_{jk_1}.$$

This beta diversity metric has been standardized by Rao to consider the average alpha diversities of the two communities to produce what is known as Rao's *H* (Rao 1982):

$$\text{Rao's H} = \frac{\text{Rao's } D_{beta}}{\left(\sum_i^{S_{k_1}} f_i \overline{\delta_{k_1}} + \sum_j^{S_{k_2}} f_j \overline{\delta_{k_2}}\right) \times 1/2}.$$

In recent years, there has been extensive debate regarding the dependence of species beta diversity metrics to levels of local diversity. In other words, species beta diversity values may not be comparable across regions where local species diversity is very different. Rao's *H* was ahead of its time in considering this possibility. However, this metric is infrequently utilized in the phylogenetic community ecology literature. Indeed, most of the above beta diversity metrics are infrequently utilized. I suspect this is partly due to the vastly increased amount of computational time necessary to calculate these metrics as well as their null models. Nonetheless, there exist several instances where they have been utilized to demonstrate instances where species and phylogenetic beta diversity have diverged in communities through space or time.

We will now consider the second major class of distance-based phylogenetic diversity metrics—nearest neighbor metrics. These metrics have a long history in ecology, dating back to at least the early work focusing on the packing and filling of niche space (Swenson and Weiser 2014) and limiting similarity theory (MacArthur and Levins 1967). Specifically, interspecific competition should be reduced as species are more dissimilar. Weaker levels of interspecific competition relative to intraspecific competition generally promote species coexistence. This has been well established in the classical coexistence literature, but these are now commonly referred to as "niche differences" in the "modern coexistence theory" literature (e.g., Chesson 2000; Mayfield and Levine 2010). While intraspecific relatedness and intraspecific trait variation often go unmeasured in community ecology, ecologists have often used estimates of in-

terspecific similarity to indicate niche differences. Individual species pair dissimilarities can be calculated, but community ecologists often seek to quantify a community-wide estimate of these differences. This is where measurements of the mean nearest neighbor distance come into the picture.

A classic question in ecology has been whether there are fixed limits to the similarity permitted in a community of coexisting species such that as more species are added to a community, the overall niche space must increase. Thus, the mean nearest neighbor distance would be consistent across communities varying in species richness. An alternative hypothesis is that, in diverse communities, niche space is partitioned more finely. Thus, communities would have decreasing mean nearest neighbor distances as communities increase in species richness. A final possibility is that species dissimilarity simply does not matter, and that mean nearest neighbor distances may decrease with increasing species richness simply due to how the metric is calculated.

As a result, there is a large literature on nearest neighbor distances with respect to traits. However, trait measurements are not always feasible to conduct in a meaningful way across communities, due to logistical reasons or a lack of knowledge regarding what traits might be those that are the best indicators of important niche differences. It is within this context that nearest neighbor metrics were translated and introduced into phylogenetic community ecology by Webb (2000). Specifically, he developed what is now called the mean nearest taxon distance (*mntd*), which finds the nearest relative of each species in a community, calculates their relatedness, and takes an average value as

$$\text{mntd} = \frac{\sum_{i}^{n} \min \delta_{i,j}}{n}, \text{where } i \neq j$$

where minδi,j is the minimum phylogenetic distance between species *i* and all other, *j*, species in the community. Originally, Webb (2000) used nodal distances to calculate minδi,j, but this value is now almost always calculated using branch length information, due to the obvious limitations associated with using nodal distances.

Abundance can be incorporated into the *mntd* metric as

$$\text{mntd.a} = \frac{\sum_{i}^{n} \min \delta_{i,j} f_i}{n}, \text{where } i \neq j,$$

again, where f_i represents the abundance or frequency of species *i*. This metric, in essence, calculates the nearest heterospecific distance for every individual in the community. Importantly, like *mntd*, the *mntd.a* metric does not consider conspecifics. The two metrics will be strongly positively correlated if

species abundance is roughly even across the phylogeny. The metrics will be very loosely positively or even strongly negatively correlated if there is strong phylogenetic signal in abundance. For example, if there is a very dominant lineage that is distantly related to all other species in the community, the *mntd.a* value will be much lower than the *mntd* value. Thus, a comparison of *mntd* and *mntd.a* can be instructive regarding the distribution of abundance on a phylogeny, just as a comparison of *mpd* and *mpd.a* can be instructive.

For the most part, nearest neighbor measures of phylogenetic alpha diversity in communities are limited to *mntd* and *mntd.a*. The functional diversity literature, however, has also utilized the standard deviation of the nearest neighbor distances in a community. The logic behind this metric is that it gets to the regularity of species spacing when not weighting by abundance and the skewness of the abundance distribution across the phylogeny when weighting by abundance. Conceptually, the regularity of species spacing and abundance along the phylogeny aligns with limiting similarity theory where low standard deviations are the expectation. I see no reason why the standard deviation of nearest neighbors cannot be applied to a phylogenetic context. The lack of use in the phylogenetic literature likely has more to do with a lack of functions in popular software packages than a level of disinterest.

Nearest neighbor metrics for phylogenetic beta diversity are generally highly correlated with species beta diversity measures such as Jaccard and Bray-Curtis. The original metric, D_{nn}, did not consider species abundances and did allow the use of zero distances indicating the presents of conspecifics in both communities, which is one reason for the strong correlations with Jaccard and Bray-Curtis. The D_{nn} can be calculated as

$$\mathrm{D_{nn}} = \frac{\sum_{\mathrm{i}}^{\mathrm{nk_1}} \min\delta_{\mathrm{ik_2}} + \sum_{\mathrm{j}}^{\mathrm{nk_2}} \min\delta_{\mathrm{jk_1}}}{\mathrm{nk_1} + \mathrm{nk_2}},$$

where minδik2is the minimum phylogenetic distance between species *i* in community k_1 and all species in community k_2. Similarly, minδjk1is the minimum phylogenetic distance between species *j* in community k_2. Finally, nk_1 and nk_2 are the number of species in communities 1 and 2, respectively.

The abundance-weighted version of the D_{nn} metric (D_{nn}') can be calculated as

$$\mathrm{D_{nn}}' = \frac{\sum_{\mathrm{i}}^{\mathrm{nk_1}} \min\delta_{\mathrm{ik_2}} \times \mathrm{f_i} + \sum_{\mathrm{j}}^{\mathrm{nk_2}} \min\delta_{\mathrm{jk_1}} \times \mathrm{f_j}}{\sum_{\mathrm{i}}^{\mathrm{nk_1}} \mathrm{f_i} \times \sum_{\mathrm{j}}^{\mathrm{nk_2}} \mathrm{f_j}},$$

again, where f_i is the abundance or frequency of species *i* in community k_1 and f_j is the abundance of species *j* in community k_2. This metric also allows the inclusion of zeros to indicate the presence of conspecifics in both communities. It should be noted that both the D_{nn} and D_{nn}' metrics can be adjusted

to exclude conspecific calculations (Kembel et al. 2010). However, I won't discuss these adjustments in detail here, as they no longer align well conceptually with traditional concepts of beta diversity. However, the adjustment may allow a researcher to quickly determine whether their low phylogenetic beta diversity values are simply due to conspecifics or not. In other words, it may allow a researcher to figure out if the low phylogenetic beta diversity is due to little to no species turnover or the replacement of species in one community by congeners in another. I will end this section with a final note on phylogenetic beta diversity metrics and whether they truly reflect what most ecologists conceive of as beta diversity. The nearest neighbor metrics will converge on zero when communities are identical. However, the pairwise metrics will not converge on zero because they calculate a pairwise distance between all members in both communities. This fact may lead many to conclude that pairwise metrics should not be considered beta diversity metrics, and I am sympathetic to this conclusion. However, I do think the pairwise metrics have a place in the literature as good indicators of overall community similarity, whether with respect to phylogenetic or functional diversity.

3.5. A Conceptual Comparison of Metrics and One Metric to Rule Them All

A question swirling through the mind of many learning about a new suite of metrics is: Which metric should I use? Uncertainty regarding which phylogenetic metric to use for an ecological study is a common concern. I am frequently asked: "What is the best metric of phylogenetic diversity?" after I provide a short course or lecture on phylogenetic ecology. Part of this uncertainty is stoked by an exponentially growing diversity metric literature where authors, frequently without evidence, proclaim that the metric they are presenting is completely novel and superior to all other metrics. In reality, most "new" metrics published in the biodiversity literature are a derivative of an existing metric or the same metric applied to a different data type (i.e., applying a functional diversity metric to phylogenetic data or vice versa), and if they are superior, they are superior for detecting a particular process or pattern that may not be of immediate concern to a given ecologist.

The answers to what the best metric of phylogenetic diversity is and what metric I should use for my study are: none and it depends. Almost unfailingly, these are the answers that no one wants to hear. Rather, we prefer that there is one tool that is superior and that can be applied in every situation. This is not a realistic expectation, and more care is required in considering what phylogenetic diversity metric to use for an ecological study. In the

following paragraphs, I will attempt to outline and reiterate some key differences between the major varieties of phylogenetic diversity metrics, placing emphasis on the ecological processes or patterns of interest. This is meant to serve as a starting point in your decision-making processes. It is not a recipe, and I would like to remind readers to be wary of any cookbook decision flow chart for choosing a phylogenetic diversity metric for your study. Further, I would like to point out that the following comparison of metrics cannot possibly discuss all possible research objectives of interest.

I will divide my discussion into three separate classes of metrics and when each might be more likely to be preferred in a study. However, prior to delving into the discussion, I will preface it by stating one very large assumption that will be made. Specifically, we will assume, for the purposes of this discussion, that related species are more similar to one another than distantly related species. This assumption is violated in many ecological data sets and it is, therefore, very controversial. I will discuss this controversy in more detail in later chapters, and why ecology might be better off abandoning the assumption. However, for now, we will utilize this assumption in order to compare classes of metrics.

The first class of metrics are those that are, typically, strongly positively correlated with species richness. These include Faith's PD metric and the Helmus *PSR* metric. The strong positive correlation may often lead ecologists to avoid these metrics and require a null model if one is to begin to infer the mechanisms underlying community assembly. However, this class of metrics may be the most preferred and best suited for conservation biology. Specifically, if one is making decisions regarding what areas to prioritize for conservation, then ideally it would be beneficial to include a metric that incorporates multiple dimensions of biodiversity. One would not want to sacrifice information pertaining to species richness simply to include information regarding the relatedness of species. If one were very keen to determine the species richness free component of biodiversity, then a null model could be used with these metrics. For example, if one has a choice to conserve one of two areas and those areas differ little in their species richness (e.g., 909 species versus 922 species), then one may want to measure the phylogenetic diversity using, for example, Faith's PD metric. The second area likely would have a higher value, but the use of a null model might show that the first area has more PD once standardizing for differences in species richness. The magnitude of this standardized difference could then be considered in light of the magnitude of species richness difference (13 species), and one could arrive at an informed and logical decision that considers multiple axes of biodiversity independently and in unison. This class of metrics may also be the

most useful for biodiversity-ecosystem function research. Specifically, they may align conceptually more with at least one of the mechanisms central to this literature (i.e., sampling effects). However, they may not align well with others (i.e., complementarity effects), and disentangling the unique contribution of relatedness to the observed patterns, as we will discuss below, may prove difficult.

The second class of metrics are the pairwise metrics. These are generally strongly correlated with one another and, as such, I will lump them together as a single class. These metrics, as noted above, give a sense of the overall dispersion of species in a community or area. Thus, they do not provide enough detail to be indicative of individual species interactions, and therefore, strong inferences about the role of biotic interactions driving ecological patterns cannot easily be made. Rather, these metrics are best used as indicators of the abiotic environment constraining species membership in an area or community. Specifically, these metrics will decrease as the abiotic environment selects for similar species that are superior in their demographic performance over dissimilar species. This has often been described as "abiotic filtering," but there is some controversy surrounding this term and some have, in effect, tried to define it so narrowly that it has almost been eradicated from the literature (Kraft et al. 2015). Whether we subscribe to draconian definitions of abiotic filtering or not, it is fair to say that a small pairwise dispersion likely is promoted by a strong abiotic selection of species.

The final class of metrics I will identify are nearest neighbor metrics. These metrics are best used for identifying the importance of biotic interactions. They align well with classic theory on the topic and focus on individual pairs and not all pairwise combinations. These metrics are not very useful for identifying the importance of the abiotic setting. Furthermore, while they focus on individual pairs, this information is typically averaged across the community. For this reason and others, additional information is likely useful for inferring the strength and importance of interspecific interactions. For example, experimentation and spatial and demographic analyses of natural communities would be useful for stronger inferences. Additionally, the strength of intraspecific interactions is not considered, generally, in these metrics. However, this is not a problem unique to the phylogenetic ecology literature.

3.6. Phylogenetic Diversity as a Stand-Alone and Complementary Metric

The nonindependence of some phylogenetic diversity metrics and species richness has been discussed in the previous section, as have approaches that

could be utilized in conservation biology to consider phylogenetically and species-based metrics of biodiversity independently. Thus, in many cases in conservation biology, the measurement of phylogenetic diversity is meant to complement measures of species richness and diversity. In community ecology, a debate exists, but it generally focuses on the use of phylogenetic diversity as a complementary metric to measures of functional diversity. In this section, I will focus on this debate.

Phylogenetic diversity or measures of relatedness have been utilized in community ecology generally as a stand-in or proxy for a measure of ecological, niche, or trait similarity. Specifically, relatedness has historically been used as a proxy for similarity. The rationale for using this proxy is that direct measurements of ecological, niche, or trait similarity between all species in a community may be less feasible to undertake than measuring the relatedness of species. Further, even in those cases where one can measure some traits for all species, for example, there may be many known or unknown traits of importance and therefore not measured. If these traits have phylogenetic signal, then a phylogenetic metric of diversity may be informative.

There is evidence in the ecological literature where measures of phylogenetic diversity appear to explain more of the variance in an ecological pattern than measures of functional or species diversity (e.g., Cadotte et al. 2008, 2009). Presumably, this is evidence that unmeasured traits and shared ancestry are a more important driver of the ecological outcome than the traits measured. This may lead some to argue that phylogenetic diversity is a superior metric and can serve as a stand-alone metric of biodiversity for ecological studies. This argument is, however, misguided from my perspective. A primary reason for this is that while phylogenetic diversity may explain more variance, we have, essentially, no information as to what ecological processes are important from this measure alone. Sure, it may indicate that unmeasured traits with phylogenetic signal are important. However, it could also mean that unmeasured traits that are convergent (i.e., that have phylogenetic antisignal) are important. We will never know which is true. Furthermore, it is impossible to know whether the result is due to the evolutionary history of one or a few or many traits that have a strong phylogenetic (anti-) signal. In sum, at best, we know that something about the evolutionary history of the species being studied is important for the ecological pattern, but we will never know what that something really is.

So, should phylogenetic diversity metrics not be used? I will argue that the answer is: no, but they are best used as a complementary and secondary metric to metrics of functional diversity. For example, our statistical models of ecological patterns should first include an independent variable or variables

related to those aspects of organismal function we believe a priori to be linked to a process driving the pattern. Next, a measure or measures of phylogenetic diversity should be added to the model to determine how much more variation these variables explain. If adding the phylogenetic information is beneficial, once considering a penalty for adding more variables to a model, then it opens up an avenue of research for the future. Specifically, the researcher is then challenged to figure out what exactly the phylogenetic information contains and how this could be measured and modeled directly. The other way in which this is useful is that it would allow an ecologist or a conservationist to at least demonstrate that phylogenetic diversity is an important variable to consider for management or conservation decisions, even if the reason for this importance is unknown. In other words, even if we don't know why the phylogenetic information is important, it likely will still be useful to consider for those making real-world decisions.

An alternative to the approach just described for complementing functional diversity metrics with phylogenetic diversity metrics is to generate a single diversity metric that can be differentially weighted by phylogenetic and trait information. In principle, one could then explore a series of different weighting values in a statistical model. The best-known differential weighting approach, called *FPDist*, was developed by Cadotte et al. (2013). This metric can be calculated as

$$\mathrm{FPDist} = \left(a\mathrm{PDist}^p + (1-a)\mathrm{FDist}^p\right)^{1/p},$$

where *PDist* is the phylogenetic distance between species, *FDist* is the distance between species in univariate or multivariate trait space, *a* indicates the relative weighting of importance, and *p* describes the nonlinearity of the relationship. When *p* is equal to 2, the system is Euclidean and *p* values must be greater than or equal to 1. Thus, a researcher could search and fit different *a* and *p* values to determine which combination best fits the ecologically dependent variable of interest. This is an interesting approach, but it has not been utilized very much in the literature, and it should be used more often. That said, it would still not inform us as to why the phylogenetic information is relevant. Rather, it would just give an indicator of whether the traits already measured are a better predictor of the pattern or whether unmeasured traits that have phylogenetic (anti-) signal are of more importance.

3.7. A Note on Phylogenetic Diversity and Ecosystem Function

Measures of phylogenetic diversity have primarily been used as a way of directly informing conservation decisions and as a method for quantifying the

similarity of co-occurring species as a means of inferring the mechanisms underlying community assembly. Given the large interest in the relationship between biodiversity and ecosystem function, and the progression in this literature from measuring species diversity toward measuring functional diversity, it is not surprising that phylogenetic diversity is now being tested as a predictor of ecosystem function (Cadotte et al. 2008, 2009; Flynn et al. 2011; Srivastava et al. 2012). While the phylogenetic diversity–ecosystem function literature is still thin, the work that has been produced has generated a great deal of interest and merits some brief discussion.

The original and most widely known examples correlating phylogenetic diversity with ecosystem function were conducted by Cadotte and colleagues (Cadotte et al. 2008, 2009). The work by Cadotte et al. (2009) utilized existing long-term biodiversity-ecosystem function experiments, constructed a phylogenetic tree for the species in an experiment, quantified the phylogenetic diversity of species in experimental plots, and correlated this with variables related to ecosystem function (e.g., biomass). The work has shown a statistically significant positive correlation, with one of the most notable conclusions being that phylogenetic diversity is in some instances actually a better predictor of ecosystem function than measures of species or functional diversity. There are many possible reasons for this result. First, introducing the evolutionary nonindependence of species refines the measure of biodiversity and therefore makes the mechanistic linkage between biodiversity and ecosystem function clearer than it is when species diversity is used as the metric of biodiversity. Second, it could be that phylogenetic relatedness contains more information about the similarity of species than what is contained in measures of functional diversity calculated based upon a few coarsely defined functional groups or a handful of functional traits. Causes of such a scenario could include that the traits measured are not the traits of the most importance for ecosystem function, and/or that phylogenetic relatedness is a better indicator of the overall similarity of species. These are interesting arguments that have compelled others to investigate the phylogenetic diversity–ecosystem function relationship, typically finding a positive relationship. They also potentially point to the importance of measuring multiple dimensions of biodiversity.

Despite the apparent success of phylogenetic diversity–ecosystem function research, there are several important conceptual and analytical issues that are outstanding. The first issue is that while the relationships are statistically significant, they may not be biologically significant, particularly the difference between the strength of the phylogenetic diversity–ecosystem function relationship versus the functional diversity–ecosystem function.

Additionally, the stronger phylogenetic diversity relationships may simply be a function of how diversity is calculated. For example, functional group richness being calculated as an integer (e.g., Tilman et al. 1997) may as a consequence be biased toward explaining less variation in ecosystem function than a continuous metric like phylogenetic diversity.

The second issue is that many of the phylogenetic diversity–ecosystem function relationships have been phylogenetically trivial. That is, are we really learning anything new or surprising or simply reiterating that ecosystem function increases upon the addition of two clades—a legume (Fabaceae) and a grass (Poaceae)? Did we really need phylogenetic information to elucidate this or did we already know it? One might point to the "stronger" statistical relationships found with the phylogenetic diversity metric as compared to, for example, functional group richness. If that is the argument, then we must consider the statistical issues raised in the prior paragraph. Thus, an outstanding challenge is to demonstrate a strong relationship that cannot be boiled down to a phylogenetically trivial underpinning. If this cannot be demonstrated, then it may prove difficult to convince researchers and managers to generate the data and infrastructure necessary to conduct their work upon the basis of phylogenetic diversity.

A related issue that we will discuss in more detail in the next chapter is that we may never really know why a phylogenetic diversity relationship with ecosystem function is stronger than a functional diversity relationship. Here, we may assume that the statistical relationships are not phylogenetically trivial (i.e., one legume and one grass). This may be considered the best-case scenario for phylogenetic diversity–ecosystem function research where the result is not trivial and explains a large fraction of the variance in ecosystem function. The question then becomes: Why is phylogenetic diversity a "better" predictor? A researcher may subsequently go out and measure a series of traits thought to be linked to demographic performance and niche differentiation and then search for phylogenetic signal in these data. If phylogenetic signal is detected, then the research may conclude that these traits are the traits driving the result. Alternatively, the researcher may conclude that since the collected traits have phylogenetic signal, other traits must have phylogenetic signal. The first argument suggests that one should then simply just measure those traits and abandon the phylogenetic approach. The second argument is flawed, as signal in one trait does not imply signal in other traits, and even two traits with phylogenetic signal need not be correlated. A final argument could simply be that some unmeasured or unknown traits are important. This is a reasonable argument, but it is unclear how useful it is operationally. As I will discuss in chapter 7, emerging functional phylogenomic

approaches may help solve such riddles, but these are beyond the scope of most research programs and certainly most managers. This leaves us in the position that there is some useful information in that phylogenetic tree, but we don't know what it is. Worse, we don't know if that information is important in other systems where we might like to quantify and apply phylogenetic diversity information. In trait-based research or functional group research, one can quantify whether adding a known group or trait impacts ecosystem function. Theoretically, this can be done with phylogenetic information where the importance of adding a particular clade matters, but this may not be transferrable (i.e., not all clades are in every system) or may end up being trivial (i.e., add a legume). In summary, we need to confront the reality that we may never know why phylogenetic diversity is a stronger predictor of a response and whether we care about ever knowing the underlying mechanism or not. I am of the opinion that we would want to know the underlying mechanism if we are interested in protecting and predicting our ecosystems into the future. To be clear, I am not recommending that ecology halt investigations into this topic, but a more critical, evenhanded evaluation of the approach is greatly needed.

3.8. Conclusions: A Reflection on the Dimensions of Biodiversity and a Place for Species Diversity

At the outset of this chapter, I stated that during the past 10 years biology has established a broad conceptual framework for biodiversity science, and that one of the pillars of this framework is phylogenetic diversity. This development has coincided with and inspired the development of my academic career. Therefore, like many others, I have been able to watch and participate in our struggle to set and reset this framework. At present many, perhaps the majority, of biodiversity scientists globally recognize three to four pillars or dimensions of biodiversity. To the surprise of some, this framework may not include species diversity at all. Specifically, biodiversity may be defined to comprise three dimensions—phylogenetic, functional, and genetic diversity.

The most powerful argument for species diversity retaining a place in our biodiversity framework is that it is tangible (Swenson 2011a). While a person hiking in a national forest may not be familiar with species concepts and how scientists variously define and describe species, they are very likely to differentiate biologically good species via their natural senses (e.g., sight, smell, hearing). Thus, they experience value and inadvertently or not quantify biodiversity by sense. They generally do not, at present, walk around with the tools necessary to quantify the genetic, phylogenetic, or functional diversity

of the species they encounter. Further, one may reasonably argue that even if they had the ability to quantify these axes of diversity during their hike, it would not register or be valued on the same level. Thus, if we remove the species diversity pillar from our biodiversity framework, we remove the one pillar with which the public interacts and which it values.

The above argument regarding the public-biodiversity interface being experienced through species diversity can be extended to those on the front lines confronting and dealing with our biodiversity crisis on a daily basis. Specifically, managers and conservationists are more likely to make their decisions upon the basis of lists of species names. In an ideal world, we would have detailed lists of the functions of species and their phylogenetic relationships, and managers and conservationists would inform their decisions upon the basis of more information (i.e., functional and phylogenetic diversity), but this information is generally not at their fingertips. Further, whether a decision-maker should elect to protect an assemblage of 70 species with a phylogenetic diversity of 245 million years versus one with 60 species and 255 million years of phylogenetic diversity is unclear from my perspective.

The removal of species diversity from our biodiversity framework would seriously retard our documentation of Earth's biodiversity at a moment in time when we need it to accelerate. While identifying and censusing the organisms in a time or space is far from trivial, particularly in the places where we need it most (e.g., the tropics), lists of species and their abundances are among the easiest and most basic facts one can collect to characterize their study system. Further, this core information can be compiled and compared across systems, helping facilitate quantitative tests of scientific hypotheses and a synthesis of biodiversity knowledge. Some of the most valuable and scrutinized data sets in ecology are "simply" lists of species and their abundances (e.g., Gentry's Forest Plot Database, US Geological Society Breeding Bird Survey). There are an increasing number of biodiversity surveys that seek to quantify the phylogenetic, functional, and/or genetic diversity of a space or time, but the infrastructure, technical ability, and funding necessary to make the required measurements are not likely to scale to the point where biodiversity scientists worldwide will be able to document these dimensions of biodiversity just as readily as they measure species diversity. Fortunately, for those interested in phylogenetic diversity, phylogenetic diversity can be measured by utilizing the lists of species and abundances generated in concert with informatics tools designed to estimate phylogenetic trees from lists of species and existing phylogenetic knowledge. Those who study functional and genetic diversity are not in such a fortunate position.

Now, I would like to defend the place of species diversity in our biodiver-

sity framework by scrutinizing the place of genetic and phylogenetic diversity. An easy starting point for this discussion would be that without knowing what a species is or documenting its presence in a study system, one would not be able to quantify the genetic diversity within said species, but let us dig deeper. Intraspecific genetic diversity and interspecific phylogenetic diversity represent two endpoints of a single axis. They need not be correlated within a single study, but they both concern the genetic dissimilarity between two individuals. That is, the average intraspecific genetic diversity across species in an assemblage need not be correlated with the phylogenetic diversity of the assemblage, but, in essence, both measures quantify the genetic similarity of two individuals drawn at random from the system. Thus, why should we consider them to be two distinct axes rather than one continuous axis? If one argues that they must be distinct, then why is species diversity as a fundamental and biologically meaningful midpoint (at least in the case of macroorganisms) not distinct? It appears to me that neither argument is infallible, and we are wise to tip the balance in favor of a more inclusive framework that recognizes the importance, past and present, of species diversity in biodiversity science.

In closing, I want to reiterate that we can understand a great deal more about our study systems and therefore help project and protect their fates by a consideration of their phylogenetic, genetic, or functional diversity than we can by measuring their species diversity. That should not, however, compel us to remove or drastically reduce the importance of species diversity in biodiversity science, if for no other reason than that it is the axis of biodiversity that is most tangible to humans.

4

Community Assembly: Phylogenies as a Proxy

The structure of ecological communities is, generally, the cumulative property resulting from the ability of individuals from different species to colonize and persist in a given location given the abiotic and biotic conditions. Those studying these processes often refer to their research as the investigation into the determinants of community assembly and/or species coexistence. The investigation of community assembly or species coexistence makes up a large share of the research conducted under the umbrella of community ecology (Mittelbach 2012). While the terms "community assembly" and "species coexistence" are often treated as synonyms, they need not, and should not, be treated as such.

Species coexistence is the investigation of pairs of species that stably coexist, or not, based upon their direct interactions with each other, indirect interactions with additional species, and interactions with the abiotic environment. Investigations, conducted on small spatial scales, into the consequences of the movement of individuals and their offspring for community structure also fall within the realm of species coexistence research programs. Species coexistence research in itself, however, typically does not seriously consider the historical, biogeographic, or evolutionary events and processes that brought a species or a lineage to the region under study in the first place (HilleRisLambers et al. 2012).

The investigation of the implications of historical, biogeographic, or evolutionary events and processes for community structure combined with the investigation of the processes dictating species coexistence constitutes the study of community assembly. Thus, the study of community assembly is informed by, but not limited to, an understanding of the processes driving local-scale coexistence. A detailed understanding of local-scale species coexistence

or a detailed account of the regional-scale historical, biogeographic, and evolutionary processes driving colonization therefore is not by itself equivalent to an understanding of community assembly. Rather, an integration of these two scales of investigation, including research into feedbacks between local and regional, is required when studying community assembly. However, it is worth noting that there is a persuasive literature arguing for a greater impact of regional-scale processes, which are less frequently studied in ecology, on the local-scale patterns typically investigated by community ecologists (e.g., Ricklefs 1987; Ricklefs and Schluter 1993).

The study of island biogeography (MacArthur and Wilson 1963, 1967) has been critical for the conceptual and analytical development of community assembly research on local and regional scales. Specifically, the dependency of island assemblage species richness on the distance and isolation of the island from a mainland source pool naturally led to the investigation of why some species from the mainland colonized an island and others did not. The first goal treated all species as effectively equivalent, while the second implicitly or explicitly aimed to determine whether species differences, particularly with respect to each other and not always the abiotic environment, were important, or whether chance events were the dominant force structuring island assemblages (i.e., determinism versus stochasticity).

The study of local-scale species coexistence within a region has been similarly entrenched in the investigation of the relative importance of deterministic versus stochastic processes, also with strong theoretical underpinnings ranging from meta-population and meta-community models grounded in island biogeography theory effectively treating individuals and species as equivalent (Hubbell 2001), to models dependent upon the inherent differences between individuals and species (see Holyoak et al. 2005).

A common analytical currency between these two scales of investigation is the degree to which differences between individuals or species influence their ability to colonize and/or coexist within a locality. More specifically, does the degree of similarity in resource use or function determine the observed community structure, or how does functional ecology inform community ecology? The classical reasoning is generally that a deterministic tension exists where species must be similar in order to coexist in an abiotic environment imposing similar constraints, but they must also be different enough to prevent competitive exclusion. Thus, similar species are expected to coexist in localities where the abiotic environment has a greater constraint on community composition (Keddy 1992), whereas dissimilar species are expected to coexist when the biotic environment has a greater influence on community composition (e.g., MacArthur and Levins 1967). However, if the community

composition is random with respect to species differences, one may infer that chance events have a greater influence. As I will discuss below, this classical inference pathway is currently being revisited in the literature in light of theoretical developments (e.g., Chesson 2000; Mayfield and Levine 2010), but, by and large, the previous and much of the current literature has used the classical approach.

Although similarity in resource use or function are critical pieces of information for most investigations of community assembly, quantifying this similarity is generally not a trivial exercise. Indeed, in many landmark investigations into community assembly, the information used to describe the similarity between species in their resource use or function is not as robust as desired (reviewed in Dayan and Simberloff 2005). Determining the aspects of organismal functional morphology and physiology that underlie species performance in a given context is, therefore, an important and ongoing grand challenge for ecology and evolution generally (e.g., Arnold 1983; Wainwright 1991) and community ecology itself (e.g., Losos 1990; Swenson 2011a, 2013).

This challenge of quantifying the species similarity in resource use and function and its importance for community assembly research has been appreciated for over 100 years, leading many to search for pragmatic approaches that may quickly, albeit crudely, estimate the similarity of species in a study system. One of, if not, the first pragmatic approaches employed in community assembly research for this purpose was to use the relatedness of species as a proxy for their similarity. The conceptual and analytical development of this proxy and its current and future usage in community assembly research is the topic of the present chapter.

4.1. Conceptual Foundations of the Phylogenetic Proxy

In the previous section, I briefly discussed the general importance of quantifying the degree of functional similarity between species and how function links to performance when attempting to infer the mechanisms underlying community assembly. Accomplishing this goal is easier said than done, and ecologists historically have sought pragmatic approaches for estimating the similarity of species. The most prominent of these has been the use of the degree of relatedness between two species as a proxy of their similarity, which I will refer to as the phylogenetic proxy. As with many foundational concepts in ecology and evolution, the rationale for a phylogenetic proxy can be traced to Charles Darwin. It was common descent and Darwin's discussion of competition between allied forms that motivated early researchers to begin to use the phylogenetic proxy when considering the assembly of communities

and the relative importance of competition. Charles Elton's classic discussion of competition and community structure (Elton 1946) relied heavily, if not entirely, on the phylogenetic proxy where he cited the following original text by Darwin (1859):

> As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera . . . We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature; but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life.

This text by Darwin forms the foundation upon which most phylogenetic analyses of community assembly, or community phylogenetics as we currently know it, is built. There are several important insights relayed in this small bit of text, but the main takeaway for most researchers is that closely related species should compete more intensely than distantly related species. Therefore, if competition, via niche differences, drives community structure, then closely related species should not coexist. Indeed, this is the framework and thought process used by Elton (1946) and in many community phylogenetics papers.

It is also informative to highlight some of the caveats and less well-scrutinized parts of the above text by Darwin. First, it is clear that Darwin recognizes that this is not a rule that applies to every scenario. Second, the text is clear that there is "some similarity" and the competition will "generally be more severe." In other words, the text does not say that closely related species are identical (i.e., no trait or niche evolution within a genus), and that again this is a general prediction and not a strict rule. Finally, Darwin states that we can "dimly see why" the proxy would work, but we would never know precisely why one species may competitively exclude another or perhaps drive another to extinction. This last comment is critically important for community phylogenetics research, where it is acknowledged that although we may find a significant phylogenetic pattern in our data, we will never know exactly why two species do not coexist even in the best-case scenario. In other words, we can never know exactly those features of organismal form and function that make one species a superior competitor simply by using a phylogenetic proxy representing the multivariate similarity between species. There is never a substitute for detailed knowledge regarding the functional ecology of the species in the study system. I will discuss the importance of this in more

detail below in section 4.5, but the immediate point here is that Darwin (1859) already recognized that, even given the assumption that closely related species are generally more similar than distantly related species and therefore they compete more intensely, we will never have the detailed information we may desire relating organismal form and function to coexistence and ultimately community assembly.

There is one last issue that is worth considering in light of Darwin's discussion of what I am calling the phylogenetic proxy. It is that in most cases true sister species tend not to co-occur locally or regionally, and if they do co-occur regionally, their geographic ranges overlap very little (e.g., Stephens and Wiens 2003; Davies et al. 2007; Pigot and Tobias 2013). Certainly, congeneric species often do co-occur, and in many cases there are more congeners co-occurring than expected, but rarely do we actually see the most closely related species to a focal species co-occurring. This phenomenon is best discussed in the context of allopatric speciation, which is generally agreed to be the predominant geographic form of speciation while stipulating that adaptive radiations on islands and/or sympatric speciation do not necessarily align well with the following discussion.

It is obvious that sister species will often not co-occur simply because they have not been able to expand their ranges enough to come back into secondary contact. However, in those cases where sister species do come back into contact, they often form abutting range margins with some level of introgression, but rarely do their ranges significantly invade one another, presumably due to competitive exclusion. In some regions, these abutting ranges are found in the same geographic location for many sister species pairs, forming what are referred to as suture zones (Remington 1968; Hewitt 2000; Swenson and Howard 2004, 2005). If we consider such instances, it would appear that Darwin's original inclinations are well supported. The most closely related species cannot co-occur, indicating perhaps that these lineages have diverged in traits related to reproductive isolation, but less so with respect to resource use. This would be particularly the case for "tension zones," where abutting range margins are dictated more by mass effects and less so on the extrinsic environment (Barton and Hewitt 1985). In other cases, the sister species have also diverged in their traits related to the extrinsic environment and resource use, as well as those traits related to reproductive isolation. The abutting range margins for these sister pairs would align along an abiotic transition, where one species or both species can competitively exclude the other due to a superior ability to survive and use the extrinsic environment (Moore 1977; Swenson 2006). In these cases, it appears clear that strong competition between sister species prevents their co-occurrence. So, an interesting and

important outstanding question is whether Darwin essentially had it right all along, but only in the context of sister species and not when considering all congeneric species pairs. That is, relatedness is indicative of competitive interactions and the ability to co-occur, but only when considering sister species that have only diverged along one or a few niche or trait axes. Thus, the ability to relate competitive interactions to relatedness becomes intractable any deeper in the phylogenetic tree, and this is perhaps why sisters cannot co-occur and congeners can co-occur. It is unclear whether this argument will hold, but it is worth strong consideration, particularly when one is thinking about the phylogeny being used as a proxy for the average or general similarity of a multivariate phenotype or niche and what this actually means or does not mean for co-occurrence and community ecology in general.

4.2. Analytical Foundations of the Phylogenetic Proxy

The usage of a phylogenetic or relatedness proxy for similarity in community ecology can be traced to the well-known Swiss phytogeographer Paul Jaccard (Jaccard 1901; Jarvinen 1982). Specifically, Jaccard devised a measure he called the "generic coefficient," which is equivalent to the ratio of genera to species in a sample (Jaccard 1901, 1926, 1940). As the generic coefficient decreases (i.e., when the number of species in a sample disproportionally increases compared to the number of genera), the sample is on average composed of species more closely related to one another than in a sample with a higher generic coefficient. For example, a sample with 10 genera and 10 species has no genus with more than one species represented, while a sample with five genera and 10 species has at least one and potentially up to five genera with more than one species represented in the sample. Jaccard reasoned, based upon his readings of Darwin (1859), that congeners were more likely to be similar and therefore compete. Thus, in an area that is relatively simple or homogeneous with respect to habitat diversity, we may expect only one or a few species per genus, due to strong interspecific competition within a genus producing a smaller generic coefficient. Conversely, in areas that are ecologically diverse or have many available habitat types, we may expect a higher number of species per genus, producing a higher generic coefficient.

Interestingly, within 20 years the generic coefficient played a central role in perhaps one of the first vigorous debates regarding the relative importance of stochastically dispersal-based versus deterministically based community assembly (Jarvinen 1982). Specifically, in 1921, the Finnish phytogeographer Alvar Palmgren published his work analyzing the floristic composition on the Åland Islands off the coast of Finland (Palmgren 1921). Palmgren noted

that the entire study system contained 324 vascular plants, but the number of species decreased eastward away from the coast. Based upon this evidence, Palmgren inferred that isolation (i.e., distance from the coast) was the critical factor dictating the observed gradient in species richness (Palmgren 1921).

Jaccard (1922) immediately questioned the inferences made by Palmgren (1921). Specifically, Jaccard (1922) argued that the decrease in species richness with distance from the coast was not simply due to dispersal, but due to a decrease in the ecological or habitat diversity with distance from the coast. This argument was buoyed by evidence presented by Jaccard that the generic coefficient increased with distance from the coast, indicating that the island floristic composition included less and less closely related species (i.e., fewer congeners on average) with the increased distance from the coast. In essence, Jaccard (1922) was reasoning that congeneric species are similar and therefore likely to compete more intensely and therefore exclude one another in a given habitat (although he did not use this terminology and his work predates Gause's foundational work on the topic [Gause 1934]), and that the only way to have many congeners in a flora was to have many habitats. In other words, Jaccard (1922) was arguing for the general importance of deterministic processes over the dispersal-based stochasticity argument developed by Palmgren (1921).

In his response to Jaccard in 1925, Palmgren highlighted two fundamental problems with Jaccard's analytical approach that likely led to flawed inferences (Palmgren 1925). First, Palmgren noted that the generic coefficient cannot be used to quickly infer ecological or habitat diversity simply because it can be invariant with spatial scale. For example, a local community with two genera and 10 species and a continental scale assemblage of 2,000 genera and 10,000 species have identical generic coefficients, but there is no doubt that the continental scale encompasses much more ecological diversity than the local scale. Thus, like any other ratio, great care should be taken in interpreting it across systems or scales. Second, Palmgren (1925) argues that the generic coefficient is necessarily correlated with species richness, such that at low species richness values the generic coefficient must be higher. In other words, Palmgren is stating that even if species randomly arrived on islands with a decreasing probability with distance, as would be expected under a strictly dispersal-based stochastic model, one would get a decrease in species richness and an increase in the generic coefficient. The challenge, therefore, becomes whether the generic coefficient quantified on islands is any different than that expected from a stochastic assembly process.

This debate between Jaccard and Palmgren conducted around 100 years ago is foundational for community assembly research on many levels. First,

it highlights that, rather than being a "new" field, community phylogenetic analyses that quantify the relatedness of species to infer assembly processes have very deep conceptual and analytical roots. Second, it provides an important entry into the ongoing debate regarding the relative importance of stochasticity versus determinism during community assembly. Finally, almost as a byproduct, the debate spurred the development of null models in biogeography and community ecology that in and of itself led to a substantial literature. In the following section, I will discuss the null modeling literature as it relates to quantifying relatedness in communities and how this literature led to more rigorous inferences.

4.3. Community Assembly, Relatedness, and Null Models

A null model, strictly speaking, is a model that generates a distribution of expected patterns where only the mechanism of interest is excluded from the model (Gotelli and Graves 1996; Gotelli 2001). This distribution is typically generated using randomization techniques that have become increasingly widespread and sophisticated given increasingly powerful hardware and software. Despite the importance of the null models implemented via computer simulations in modern community assembly research, the first null model simulations in community ecology occurred in the 1920s by Arthur Maillefer. Perhaps not coincidentally, Maillefer's interest in null models concerned Jaccard's generic coefficient and began with a purely mathematical exercise (Maillefer 1928). Specifically, Maillefer began by building off the recent publication by Willis and Yule (1922), which argued that globally the number of species per genus followed a log-log relationship, where many genera had few species and a few genera had many species. This general relationship could be simply characterized mathematically as

$$\log g(s) = b\log(s) + a,$$

where s is the number of species and $g(s)$ is the number of genera with s species with a negative slope ($-b$) and a positive intercept (a) (Jarvinen 1982). Maillefer (1928) demonstrated that if species were proportionally reduced across all genera, then b increases, indicating a necessary mathematical relationship between species richness and the generic coefficient. In 1929, Maillefer expanded on this foundation to demonstrate the expected generic coefficient value for a given species value (Maillefer 1929). To accomplish this, Maillefer conducted what is believed to be the first null model simulation study in ecology (Jarvinen 1982). Specifically, he used the list of species in the Swiss flora, constituting 2,575 species in 695 genera. He then labeled 2,575 cards each with

a unique Latin binomial from the flora. Next, he randomly drew cards and calculated the generic coefficient of the sample as the number of cards (i.e., the species richness of the sample) increased. The result of the simulation is a strong negative relationship between species richness and the generic coefficient, just as Palmgren (1925) had proposed. Due to a lack of a computer, Maillefer was unable to perform many replicates per species richness level and therefore unable to provide a robust estimate of the distribution of generic coefficients expected for a given species richness level. However, such a simulation is now quite easy. For example, we may assume a lognormal distribution of the number of species per genus for 1,000 species and 63 genera in a study system (fig. 4.1).

Next, for community species richness levels 1 to 100, species are randomly drawn without replacement and a generic coefficient is computed. This is replicated in this example 999 times per community species richness level to provide a distribution of expected generic coefficients for a given species

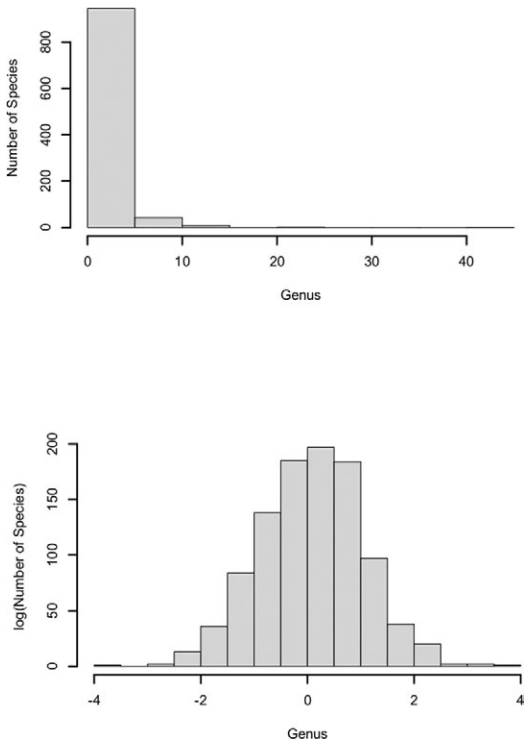


FIGURE 4.1. A randomly generated lognormal distribution of species richness (*y*-axis) per genus (*x*-axis) used for a simulation depicting the expected genus-to-species ratio for a given level of community species richness. The top panel is the nonlogged distribution, and the bottom panel is the logged distribution of the same data.

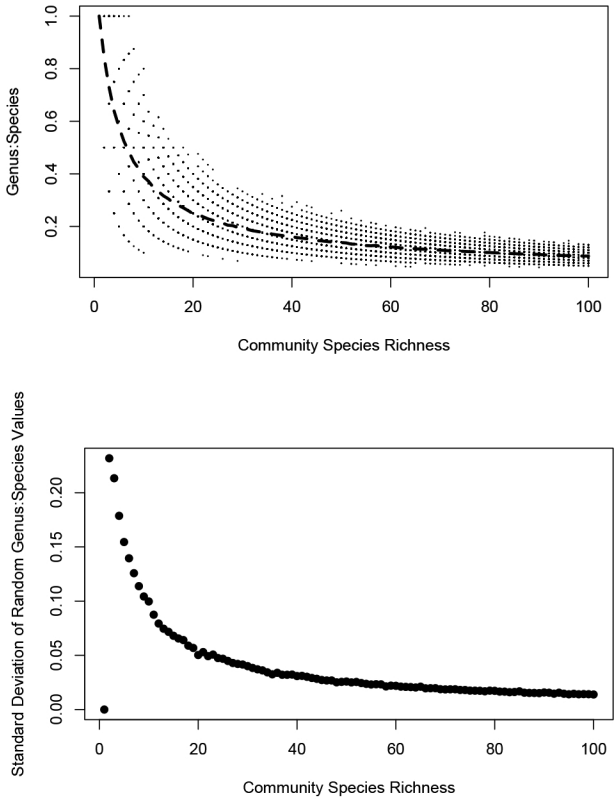


FIGURE 4.2. The top panel depicts the expected distribution of genus-to-species ratios (*y*-axis) for a given level of community species richness. A total of 999 simulations were run per community species richness level, where species were selected at random without replacement from the lognormal distribution shown in figure 6.1. Each individual point is a simulation, and the dashed line is the mean value. The bottom panel shows the expected standard deviation of genus-to-species ratios for a given level of community species richness. A species richness of one can only have one genus-to-species ratio, but species-poor communities with more than one species have a far larger range of possible genus-to-species ratios than more species-rich communities. Thus, the panels demonstrate that, as Jaccard (1940) states, there is more than one possible genus-to-species ratio value per level of species richness, but the trend in this ratio with richness and the decline in the variation in expected values necessitates a null modeling approach.

richness level (fig. 4.2), which follows the hypergeometric distribution described previously by Heck et al. (1975). The observed generic coefficient can then be placed in this distribution to estimate the probability that the observed value is greater or lower than that expected randomly or by quantifying if it is within two standard deviations of the mean if the distribution of null generic coefficients is normal.

Maillefer (1929) also used his simulation to explore generic coefficients in regions around the world, though primarily in the temperate zone, as they

compare to a null expectation. While unable to generate full null distributions where *p* values could be calculated, Maillefer found that the observed generic coefficients were generally lower than the null expectation derived from the simulation (Maillefer 1929). In other words, he tended to find evidence for more congeners than expected in floras.

It is worth noting at this point that Jaccard continued to use his generic coefficient values (Jaccard 1926, 1928, 1940) without comparing them to a null expectation in his investigations, subsequent to the critique levels by Palmgren (1925) and Maillefer (1928, 1929). His rationale for this was simply that the generic coefficient can be varied for a given species richness value. This is, of course, true (see fig. 4.2), but this argument knowingly or unknowingly ignores: (a) the general trend across species richness values; and (b) that statistical distributions have variation and the observed test statistic needs to be placed into this context to detect whether it is indeed an unusually high or low value.

Palmgren and Maillefer also failed to detract other well-known users of the generic coefficient or its inverse, the species-to-genus ratio; specifically, Elton's well-known investigation inferring the general importance of competition from a general observation of few species per genus in species assemblages (Elton 1946) and Moreau's inference of competition in African bird assemblages from the low numbers of coexisting species given the number of genera (Moreau 1948, 1966). However, in both instances, Williams demonstrated that the failure of the work to consider a null distribution hindered the inferences (Williams 1947, 1951, 1964). Specifically, like Maillefer (1929) before him, Williams demonstrated that species in assemblages were actually more closely related than expected by chance, thereby providing evidence in direct opposition to the original inferences. While it seems clear that Elton and Moreau, and certainly Jaccard, opposed null models incorrectly on a conceptual level, and some have argued that there has been a historical resistance to true null hypotheses in ecology (see MacFadyen 1975; Strong 1980), the difficulty in generating null distributions was likely also to blame for a lack of null models at this point in time.

Beyond simple computational limits, additional concerns regarding null model implementation came to the fore in the 1970s and are still present today. These concerns were less focused upon whether a null model should be used, and more on how they should be constructed. In particular, many of the most substantial discussions did, and still do, revolve around from what appropriate source species pool a random assemblage of species should be drawn (Simberloff 1970; Strong et al. 1979; Grant and Abbott 1980; Colwell and Winkler 1984; Swenson et al. 2006; Cavender-Bares et al. 2006; Lessard

et al. 2012). The species pool can be, and often is, defined as the species that could potentially colonize the locality being studied. Immediately upon consideration of this conceptual definition, it becomes clear that it is very ambiguous operationally. Putting aside the difficulty of knowing the dispersal capabilities of all the species in a region, there are several problems when it comes to defining an "appropriate" species pool. For instance, one must confront the obvious questions regarding the spatio-temporal scales of interest. Are we primarily concerned with the ability of species to colonize within the last several millennia or the last several thousand years, or the ability of a single individual to disperse to the site during its lifetime? The desired time scale will, of course, depend on the actual biological question being addressed, making a single operational definition to be used in all studies impossible given the broad conceptual definition. An additional complication with a general source pool definition particularly applicable to island systems is that many lineages likely have colonized and diversified. In other words, not all species presently observed dispersed to the archipelago or study region. Rather, they have originated at that location. Thus, it might be more preferable to quantify whether the number of unique colonization events, irrespective of subsequent diversification, from a given lineage is higher or lower than expected given the mainland lineage source pool. In sum, the conceptual definition of how to construct a source pool for null model analyses in community ecology research is simple to state and can be very challenging to implement, and the answer to "What species pool should I use?" should always be answered with "It depends on your question."

Along with the difficulty of implementing the conceptual definition of a species pool in null modeling analyses, there are the unintended consequences of how the species pool composition itself influences one's ability to detect the ecological process of interest (Simberloff 1970). That is, seemingly minor or harmless decisions regarding the composition of the species pool might have a substantial influence on Type I and Type II error rates. This issue did not elude researchers during the null modeling debates of the 1970s and 1980s. For example, Colwell and Winkler (1984) used a simulation approach to demonstrate that defining a source pool that is unrealistically large increases the probability of rejecting a null hypothesis. In community phylogenetics, this generally leads a researcher to find species that are more closely related than expected (Cavender-Bares et al. 2006; Swenson et al. 2006; Kraft and Ackerly 2010). Conversely, an overly restrictive species pool decreases the statistical power of a researcher to detect any nonrandom patterns in the data (Colwell and Winkler 1984). In addition to the biases demonstrated by Colwell and Winkler (1984), there is the consideration of the probability with

which a species could be drawn from a source pool. Specifically, a simple null model could be that all species could be drawn with an equal probability until the observed local species richness is achieved. A problem with this model is that one of the few general laws in ecology is that there are many rare and few common species, leading to roughly lognormal species abundance distributions (Preston 1960). Thus, it may be more reasonable to assume that a common species has a greater probability of colonizing a locality than a rarer one, and that species should be drawn from the source pool with a probability equivalent to their regional-scale relative abundances. Null models that fix the number of sites occupied by a species in a region and the number of species observed in local assemblages to generate null local assemblages (e.g., independent swap null models) are now easily implemented to deal with such issues, but this was not the case until recently (Gotelli 2001). Investigations that have been done comparing null model algorithms have shown that simple null models that only fix the observed local species richness and do not draw species based on their regional occupancy rates (i.e., the number of communities occupied by a species in the meta-community) are prone to inflated Type I error rates (Kembel and Hubbell 2006), and that the phylogenetic distribution of relative abundance itself can bias null model results (Hardy 2008).

Thus, perhaps the most important and difficult decisions a community assembly researcher can make during their analyses are the composition of the species pool and the algorithm utilized to construct the null assemblages. It is at this point that it is worth revisiting the purpose of a null model. As defined above, a null model is a model that generates patterns given the observed data, excluding the process or pattern of interest (Gotelli 2001). In other words, all observed patterns in the data should be fixed in null model simulations and only the pattern or process of interest should be free to vary. In so doing, one can make clearer and less biased inferences about the pattern or process of interest while acknowledging that there are likely other observed variables that were not observed and therefore not fixed in the null model simulation, which may themselves bias the inference. The earliest null models generally only fixed one of the many observed patterns in the data, the observed local species richness, while the pattern of interest, the local community composition, and many other patterns not of immediate interest, such as the regional occupancy rates of species, were free to vary in the simulations. This undoubtedly produced inflated Type I error rates. This approach was, however, understandable early on, given the difficulty in simulating null communities with so many fixed parameters. Currently, this approach should not be taken and researchers should be increasingly

pushed to recall what a null model is and is not and that, when possible, all observed patterns in the data should be fixed except the pattern of interest. The downside of this strict approach is that there may be only so many ways to randomize a data set with so many fixed parameters, giving a researcher very little or no power to detect a nonrandom pattern even if one exists (see Kraft et al. 2007; Swenson and Weiser 2014). This is particularly the case when randomizing the spatial distribution of individuals and species in ecological data sets. For example, most null modeling approaches randomize community data matrices where the species in the species pool are in columns and the local assemblages are in rows, with values in the matrix representing presence/absence or some measure of abundance. Popular algorithms, such as the independent swap, that randomize community data matrices while fixing the local species richness (i.e., the row sums after the matrix is converted to a presence/absence matrix) and the regional occupancy rate of a species (i.e., the column sums after the matrix is converted to a presence/absence matrix) can be very constrained in the number of possible random realizations to the point where a researcher may be finding random patterns simply because they have no statistical power.

Along with the above issues is the fact that algorithms such as an independent swap that fixes occupancy rates will never include a species to be in a random assemblage that isn't in an observed assemblage, and the spatial relationships between local assemblages are not considered. It is difficult to know if the first problem is a "real" problem, in that the species could simply not be in any local assemblage because it couldn't colonize and therefore should not be in the species pool, or whether it could colonize but was restricted from doing so due to some biological process of interest. The second problem, however, I consider to be much more insidious for community ecology. In particular, if a species has a clumped spatial distribution perhaps due to dispersal limitation and it only occupies three of the 100 localities in the region being investigated, an independent swap null model will ensure that it occupies three localities in each iteration of the null model, but these three localities could be very spatially segregated. Thus, not only was local community composition varying, but the degree of spatial aggregation was also varying. Given the importance of dispersal limitation for major ecological theories of interest (i.e., Neutral Theory; Hubbell 2001), it is problematic to have such a null model. At the same time, a null model that fixes the observed local species richness, regional occupancy rates of species, *and* the regional spatial aggregation of species would likely have at best very little power to detect nonrandom patterns of community composition unless the study

was perhaps conducted on a continental scale with very finely defined local assemblages.

It is for the above reasons that I often feel more comfortable with a null model that randomizes the relatedness of species (i.e., their phylogenetic position) rather than one that randomizes the community data matrix (e.g., Swenson, Erickson, et al. 2012; Swenson, Stegen, et al. 2012). In other words, simply randomizing the names of species on the tips of the phylogeny fixes all observed patterns in the community data matrix during each iteration of a null model while only varying relatedness. Most studies of relatedness and community assembly are primarily interested in the relatedness of co-occurring species, and this null model allows this to vary while fixing all spatial patterns. Some have suggested that such null models may have inherent biases when the regional occupancy rates or relative abundances of species have phylogenetic signal, but such issues can be adequately dealt with via more refined name-shuffling algorithms that do not alter the observed community data matrix (Hardy 2008). In sum, while there is no perfect null model, I would argue that it is generally preferable to avoid randomizing complex spatial data *in lieu of* randomizing a key parameter of interest such as relatedness.

In this section, I have presented a brief history of null models in community assembly. This history began and still largely revolves around the analysis of relatedness in communities to infer community assembly and coexistence mechanisms. Although the literature on this topic is much larger than what I have covered here, the issues covered should provide a strong basis for understanding and interpreting null models. Debates regarding null models will continue and be more refined, and robust models will be produced, but the key tenets that will persist are that: (a) there are no perfect null model algorithms or null model parameters (i.e., source pools) for every ecological study; and (b) a researcher must try their best to fix all observed patterns but the pattern of interest while balancing the trade-off between the number of fixed parameters and statistical power.

4.4. The Rebirth of Relatedness and Co-occurrence in a Bornean Rain Forest

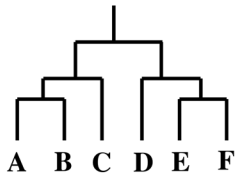
As we approached the new millennium, the quantification of relatedness in ecological communities in order to infer the degree of similarity between co-occurring species and ultimately the mechanisms underlying co-occurrence and community assembly had largely come to a halt. There are likely many reasons for this decline, but the acrimonious literature regarding null models

no doubt contributed more than its share to the death of taxonomic ratio (e.g., genus-to-species ratio) analyses. Indeed, it may have seemed impossible in the 1990s that what is now known as "community phylogenetics" would be as popular a subfield as it has become today.

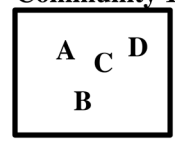
It was in this environment in 2000 that Cam Webb reinvigorated interest in relatedness with respect to community ecology by suggesting two novel approaches (Webb 2000). First, Webb pointed out that most taxonomic ratio research had been conducted on large spatial scales for the purpose of making inferences about community assembly, while the analysis of relatedness on local scales had a much shallower or nonexistent literature. Second, he noted that a fundamental problem with taxonomic ratios is their lack of detailed information about relatedness between co-occurring species deeper in the phylogeny. In other words, a genus-to-species ratio provides information about co-occurring congeners, but not, for example, confamilial species. Thus, important information had been lacking in previous taxonomic ratio research that could be used to refine inferences. Webb set out to address these issues while simultaneously examining the structure of tree communities in a Bornean rain forest.

The Webb (2000) paper begins with a forceful argument for the phylogenetic proxy in community ecology, citing classic works from the comparative methods literature that have previously described the propensity of closely related species to be similar (e.g., Brooks and McLennan 1991; Harvey and Pagel 1991). Webb's text was careful to point out that relatedness is being used to indicate the overall similarity or average similarity of two species and not the similarity of each and every trait or niche axes of the two species. Further, the text clearly acknowledges instances where this general assumption will likely fail (e.g., island radiations; Losos et al. 1998). In weighing these realities, Webb (2000) makes a final pragmatic argument that it will likely often be impractical to measure all relevant traits or niche axes in an assemblage, particularly when working in high-diversity systems. Ultimately, this text remains one of the most carefully worded and thoughtful explanations of why the phylogenetic proxy is being employed in community ecology and how it may be interpreted or misinterpreted.

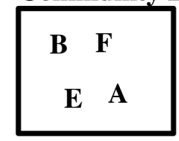
Upon establishing an argument for why and how a phylogenetic proxy may be used in community ecology, Webb introduces four novel metrics of phylogenetic community structure that are still the most widely used today (though with minor modifications). The first two metrics are quantifications of the phylogenetic diversity in the assemblage—the mean pairwise nodal distance (*mpd*) and the mean nearest nodal distance (*mnnd*) (fig. 4.3). These descriptive measures were designed to represent the overall (i.e., basal)



Community 1



Community 2



Greatest possible **mean pairwise nodal distance for 4 species = 3.66 (A, B, E, F)**

Greatest possible **mean nearest nodal distance for 4 species = 2.00 (A, C, D, F)**

Nodal Distances

	A	B	C	D
A	-	1	2	4
B		-	2	4
C			-	3

Nodal Distances

	A	B	E	F
A	-	1	5	5
B		-	5	5
E			-	1

Mean Pairwise Nodal Distance	**(1 + 2 + 4+ 2+ 4+ 3) / 6 = 2.66**	**(1 + 5 + 5+ 5+ 5+ 1) / 6 = 3.66**
Net Relatedness Index	**1 – (2.66 / 3.66) = 0.273**	**1 – (3.66 / 3.66) = 0.0**
Mean Nearest Nodal Distance	**(1 + 1 + 2+ 3) / 4 = 1.75**	**(1 + 1 + 1+ 1) / 4 = 1.0**
Nearest Taxa Index	**1 – (1.75 / 2.0) = 0.125**	**1 – (1.0 / 2.0) = 0.5**

FIGURE 4.3. Adapted from Webb (2000) to demonstrate how the original mean pairwise nodal distance (MPD), mean nearest nodal distance (MNND), net relatedness index (NRI), and nearest taxa index (NTI) were conceptualized and calculated. At the top are two communities. In the middle is a phylogenetic distance matrix based upon the number of nodes separating those species found in the community using the phylogeny on the left. In the table at the bottom are the actual calculations for the four metrics.

phylogenetic diversity of the assemblage and the distance to closest relatives (i.e., terminal), respectively. The former is likely more closely aligned with the environmental filtering of similar phenotypes, and the latter likely more indicative of the strength of negative interactions between closely related species and therefore more akin to measures such as the genus-to-species ratio. These two descriptive metrics were then compared to a maximum possible value given the number of species in the sample to produce the Net Relatedness Index (*NRI*) and the Nearest Taxa Index (*NTI*), respectively (fig. 4.3). In other words, Webb realized that the observed *mpd* and *mnnd* could not be interpreted without comparing them to an expected value.

The *NRI* and *NTI* metrics were then applied to a series of 40 x 40m tree inventory plots installed by Webb in Borneo. The implementation of *NRI* and *NTI*, though, was slightly different from Webb's conceptual figure (fig. 4.3), as a randomization was used to estimate the maximum *mpd* and *mnnd* of each assemblage and it did not directly know the exact maximum *mpd* and *mnnd* possible. The randomizations fixed the observed species richness in each sample and the occupancy rates of species across all samples in the study system (i.e., an independent swap null model). The general result

from this work was that closely related species tended to co-occur, which was tentatively interpreted as evidence of soil habitat partitioning (Webb 2000). A series of sensitivity analyses regarding phylogenetic resolution and randomization type were also performed that generally demonstrated that the initial results were robust.

Not long after Webb (2000), the seminal review by Webb et al. (2002) was published, which laid a broader and stronger foundation for the emerging field of community phylogenetics. Out of the many important conceptual and analytical advances presented in Webb et al. (2002), three stand out. First, the review discussed a multi-scale research program that detailed the importance of phylogenetic information for community ecology from biogeographic to very local scales, which represents a formal bridging of the classic taxonomic ratio literature and Webb (2000). Second, the review embraces the fact that traits or niches may not in many cases have phylogenetic signal and, indeed, they may be convergent. From this, the authors presented a now widely known table depicting the expected pattern of phylogenetic relatedness given the pattern of trait evolution and the dominant ecological force (table 4.1).

Third, the review refined the *NRI* and *NTI* metrics to incorporate phylogenetic branch lengths instead of nodal distances and to become proper effect sizes. Specifically, the observed *mpd* or *mnnd* based on branch lengths was compared to the mean *mpd* or *mnnd* from 999 randomly generated assemblages and divided by the standard deviation of the 999 random *mpd* or *mnnd* values. These three innovations and the development of the biodiversity informatics software Phylomatic (Webb and Donoghue 2005), which made constructing crude phylogenetic trees with branch lengths for any plant assemblage possible, set the foundation for an explosion of research into the phylogenetic structure of communities. In the remaining sections, we will discuss the resulting literature and future prospects.

TABLE 4.1. Patterns of phylogenetic relatedness given patterns of trait evolution and community assembly mechanisms

	Trait evolution	
Ecological process	*Conserved*	*Convergent*
Abiotic filtering	Phylogenetic clustering	Phylogenetic overdispersion
Biotic interactions	Phylogenetic overdispersion	Phylogenetic clustering or random

Note: Adapted from Webb et al. (2002), where the model of trait evolution describes the columns, the ecological process describes the rows, and the cells are the observed phylogenetic pattern. A similar graphic with rows and columns flipped can be found in Cavender-Bares et al. (2004), and a modification including random phylogenetic patterns was published by Kraft et al. (2007).

4.5. Phylogeny, the Multivariate Phenotype, and Challenging the Proxy Assumption

The review article by Webb et al. (2002) discussed how patterns of community phylogenetic structure should be dependent upon ecological process and the pattern of trait evolution (table 4.1). In doing so, they demonstrated how community phylogenetics could potentially be free from assuming phylogenetic signal in trait or niche data. Although there were previous well-known examples of convergent trait evolution driving community structure (e.g., Losos et al. 1998), it was not long until the exact framework proposed by Webb et al. (2002) was put to the test. This foundational work was conducted by Jeannine Cavender-Bares and colleagues using phylogenetic, co-occurrence, and trait data for *Quercus* (oak) species in Florida (Cavender-Bares et al. 2004). The work starts by reiterating the framework by Webb et al. (2002) in a graphical format, making it easier to visualize exactly how difference in trait evolution may result in the opposing expected pattern of community phylogenetic structure even if the assembly mechanism is the same (fig. 4.4).

Although there were numerous interesting results in the Cavender-Bares et al. (2004) paper, the findings that are generally cited are that distantly related species tended to co-occur and that some traits were convergent while others had phylogenetic signal. Further, those traits that, roughly, had phylogenetic signal were dissimilar between co-occurring species, while those that were convergent tended to be similar between co-occurring, ultimately giving a pattern of phylogenetic overdispersion. Thus, the observed nonrandom community phylogenetic pattern was the emergent result of two different ecological processes, abiotic filtering and biotic interactions, acting on different traits with different evolutionary histories. Suddenly, it became apparent to community ecologists seeking to use a phylogenetic proxy in their research that the inference pathway from phylogenetic pattern to ecological mechanism was more treacherous than originally believed.

One impact that the work by Cavender-Bares et al. (2004) had on the literature was that researchers were now obliged to demonstrate the presence of phylogenetic signal in trait data, or the lack thereof, for their study system in order to infer an assembly process from the phylogenetic pattern. At this point, community phylogenetics entered the strange land of using a phylogenetic proxy to avoid having to measure traits, while simultaneously measuring those traits and phylogenetic signal in those traits to support inferences derived from the original phylogenetic pattern. In other words, we

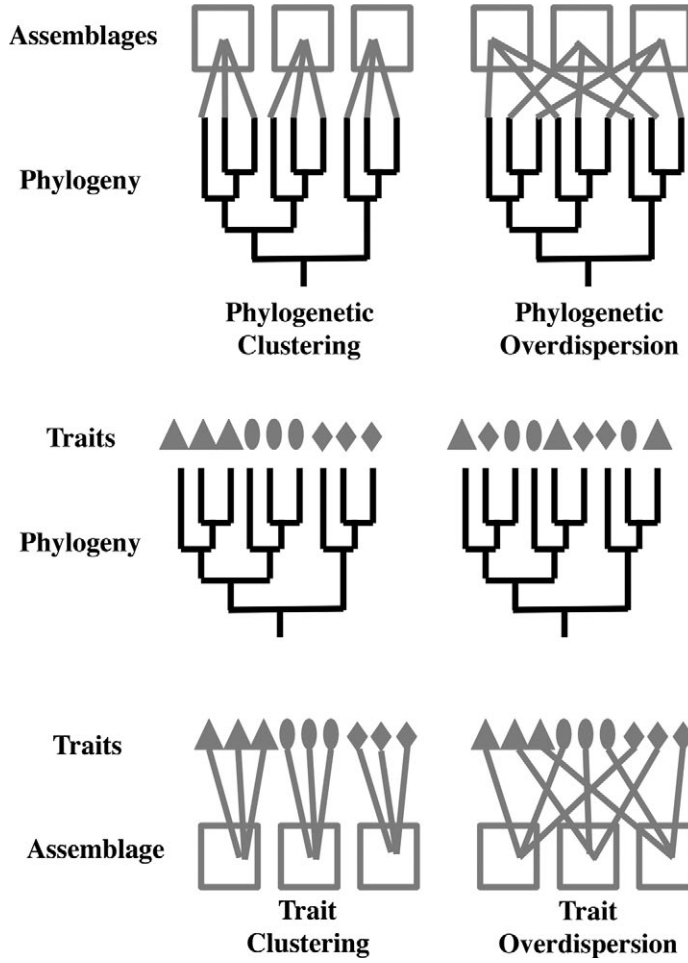


FIGURE 4.4. Adapted from Cavender-Bares et al. (2004) to graphically demonstrate how differences in trait evolution and ecological processes may interact to give a phylogenetic pattern (table 4.1). The bottom row indicates whether species with similar traits coexist (left) or not (right), presumably due to abiotic interactions or biotic interactions, respectively, being relatively more important for structuring the communities. The middle panel depicts conserved (left) and convergent (right) trait evolution. In the top panel are the possible community phylogenetic patterns. The top right pattern of phylogenetic overdispersion could result from trait clustering and trait convergence or trait overdispersion and trait conservatism. The top left pattern of trait clustering could result from trait clustering and trait conservatism and potentially trait overdispersion and trait convergence.

were using a phylogeny to avoid measuring traits only to measure traits. At this point, it became rather unclear why the phylogeny was being used in the first place, and it became what I have previously called a "phylogenetic middleman" (Swenson 2013).

The work by Cavender-Bares et al. (2004) and subsequent work demon-

strating that simultaneous nonrandom trait clustering and overdispersion on different trait axes that all have phylogenetic signal may give rise to random community phylogenetic patterns (e.g., Swenson and Enquist 2009), and that measures of phylogenetic diversity often do not match measures of functional diversity for the same assemblage, cast serious doubt on the use of phylogenetic proxies in community ecology. The doubts regarding the usage of the phylogenetic proxy remain strongly in place today, due to the increasing evidence that either a certain series of traits does not have phylogenetic signal or the phylogenetic pattern is difficult to align with a particular ecological process.

At this point, I would argue that it is worth revisiting what was detailed in Webb (2000) and how this relates to community ecology and even the quote by Darwin himself that I provide in section 4.1. As I noted above, Webb (2000) was very careful to describe the phylogenetic proxy as a way to pragmatically estimate the average similarity of two species. Thus, from my interpretation of his text, he was never stating that every trait would have phylogenetic signal and only that the multivariate phenotype or multidimensional niche of two species would be more similar on average the more closely related they are to one another. This mirrors the argument from Darwin (1859) regarding allied forms, and it is not a difficult concept for the average biologist to understand when presented on an absurd scale (i.e., two whales are more similar to one another on average than one whale is to a mouse). However, most of us can detail certain "ecological synapomorphies" that apply to far less trivial examples, such as the general growth habit differences between the two large genera in the plant family Piperaceae, *Peperomia* and *Piper*. This is very different from saying all *Piper* are the same. Rather, it is saying that generally *Piper* are herbs, shrubs, or trees, while *Peperomia* are, generally, epiphytic. On the other hand, there are classic examples of convergence (e.g., Euphorbiaceae and Cactaceae) and genera that are fantastically diverse in their structure and function.

So, does the phylogenetic proxy actually represent the average trait or niche similarity of species, and how is that applicable to community ecology? Losos has forcefully argued that phylogenetic signal in trait and niche data should never be assumed and should be tested from the outset (Losos 2008). This, of course, makes sense, as any assumption should be tested whenever possible and should not be blindly accepted. Further, it is clear that, just like our perception of community structure given a null model analysis, our perception of phylogenetic signal is scale dependent. That is, an *Anolis* lizard is an *Anolis* lizard, generally speaking, when you compare it to all other lizards, in that it has a dewlap used for signaling and toe pads lined with lamellae, but

it is well known that within the genus *Anolis* there is a wonderful diversity of form and function, with documented linkages to the differential performance of species in a given habitat (Losos 2009). In other words, an *Anolis* is an *Anolis* and that may or may not be interesting, but it is the differences between the species in *Anolis* that dictate their local distribution and abundance. This is a fundamentally important point, particularly when we think about how two species may coexist. Liebig's Law of the Minimum and classical niche theory tell us that two species must be divergent along at least one niche axis related to resource use in order to coexist (MacArthur and Levins 1967). Given this, we must ask ourselves how useful it is to know if two species are roughly 90% similar whereas two other species are roughly 50% similar when it comes to questions regarding coexistence and assembly. It is very possible that the 10% that is divergent between two species represents the divergence along the niche axis that promotes their ability to coexist. This conceptually aligns with how we believe species diversify and evolve, where closely related species are similar due to common descent, but also diverge along a few trait or niche axes that dictate distributions and abundances.

In this light, it can be reasonable when considering large taxonomic scales to state that on average closely related species are generally more similar to one another than are two distantly related species. This could be generally useful for providing initial insights into why major lineages may be found in one place or another on larger spatial scales. Further, this also suggests that measures of phylogenetic diversity are still generally useful for conservation biology (e.g., Faith 1996), and for estimating the overall trait or niche diversity in a given assemblage broadly defined taxonomically (Cadotte et al. 2013). However, when we consider local-scale co-occurrence and particularly the co-occurrence of very closely related species, we will frequently be misled even if the phylogenetic proxy tells us with 90%–95% accuracy how similar two species are in their traits or niches, and this only reinforces Darwin's original point that we will never know exactly why two species do or do not coexist just from knowing their degree of relatedness (Darwin 1859).

4.6. Scale (Still) Matters

Along with the initial explorations regarding whether traits or niches have phylogenetic signal and the implications of this for inferring process from phylogenetic community structure was the interest in how phylogenetic community structure varies with scale. The most obvious scale of interest was spatial scale, with respect to both the spatial scale of the local assemblage

being analyzed and the spatial scale of the source species pool used for null model analyses (e.g., Tofts and Silvertown 2000; Cavender-Bares et al. 2006; Kembel and Hubbell 2006; Swenson et al. 2006, 2007). For example, my first published foray into community phylogenetics was to demonstrate that local assemblages of trees in the El Yunque National Forest in Puerto Rico appeared to be increasingly phylogenetically clustered as I redefined the species pool from the trees found immediately around the local assemblage to all species in the National Forest to all tree species in Puerto Rico and finally to all species in Puerto Rico and the US Virgin Islands. The general finding in my work on spatial scale and most other investigations of this nature has been that smaller local assemblages tend to look more phylogenetically overdispersed (i.e., more distantly related) than expected given a statically defined species pool, and that increasing the size of species pools tends to make statically defined local assemblages look more phylogenetically clustered (i.e., more closely related) than expected.

Although it was not well acknowledged in many of these early papers and is still often ignored in more recent papers, spatial scale dependency had been discussed thoroughly during the null modeling debates of the 1970s and 1980s, and the scale dependency in phylogenetic structure was completely predicted by those early works (e.g., Colwell and Winkler 1984). Thus, we probably should have already known the result of the spatial scale studies we embarked upon, but perhaps it was worthwhile to explicitly demonstrate that the same issues apply in community phylogenetics as those in taxonomic ratio null model analyses.

Taxonomic and size scaling axes were also considered early on in community phylogenetics. This work, again, produced fairly consistent results across study systems. For example, both Jeannine Cavender-Bares and I found that as the taxonomic scale of the assemblages studied increased (i.e., from a single genus to all angiosperms), the degree of phylogenetic overdispersion detected decreased (Cavender-Bares et al. 2006; Swenson et al. 2006). In other words, the phylogenetic scale of a study has a large impact on a researcher's perception of the mechanisms underlying community structure. Again, this was a reality not lost on earlier researchers (e.g., Grant and Abbott 1980). Additional scaling analyses of multiple Neotropical tree plots has shown that the phylogenetic structure of large size classes is generally overdispersed and increasingly clustered toward smaller size classes (Swenson et al. 2007; Gonzalez et al. 2010).

In 2007, I attempted to synthesize all of these scaling axes to produce a graphical expectation of how the phylogenetic structure of an assemblage is

likely to change. This work was inspired by a similar approach taken a decade earlier by Evan Weiher and Paul Keddy to conceptualize scale dependency in trait dispersion (Weiher and Keddy 1995). Vamosi et al. (2009) provided a similar concept where they considered taxonomic scale and the spatial scale of local assemblages simultaneously. In their figure, they define a Darwin–Hutchinson Zone at fine taxonomic and spatial scales, where closely related species are likely to directly interact. This, to Vamosi et al. (2009), was described as perhaps the optimal scenario for community phylogenetics investigations. While I don't completely agree with this suggestion, the Vamosi et al. (2009) graphic was a useful way of relating what type of scaling parameter space had been explored up until that time.

Scale dependency investigations in community phylogenetics can be summed up with the following. First, many of the scale dependencies had actually been predicted or demonstrated decades prior, and perhaps the emerging literature should have been more cognizant of this foundational work. Second, almost all results were scale dependent, making it difficult to compare and contrast the results across systems. Third, different processes often have different relative levels of importance on different scales, and this must be considered when structuring an analysis. Finally, it is generally more useful to conduct the research on multiple scales, so studies can be compared and scale dependencies in ecological processes can be appreciated and dissected. For example, it is nonsensical to state that community structure is the result of processes occurring on a particularly spatial or temporal scale and therefore all research must be conducted on those scales. Rather, it makes far more sense to adopt a research program that explores different scaling axes to quantify when and why different processes are relatively more important.

4.7. Recent and Current Approaches in Community Phylogenetics

Quantifying and interpreting scale dependency as it relates to phylogenetic relatedness in communities was one of the main thrusts of early research after Webb's landmark papers. Hundreds of papers were subsequently written, making inferences about community assembly processes using patterns of phylogenetic relatedness that were on occasion coupled with measures of phylogenetic signal in trait data and/or functional trait dispersion (see Cavender-Bares et al. 2009). Initially this work largely came from the plant literature, likely due to the fact that the Phylomatic tool for quickly building community phylogenies for plants made the field more accessible for plant ecologists (Webb and Donoghue 2005), but increasingly the literature

has included zoological examples, and it has become increasingly clear that microbial ecology has itself been doing community phylogenetics analyses in parallel for years. Covering the breadth and depth of this literature and discussing all of the interesting papers that have resulted would constitute an entire book by itself. Thus, in the following, with advance apologies to my colleagues whose work I do not cover, I will highlight a couple of what I consider to be key developments, with an admitted bias toward plants. I will also not cover the advances made with respect to how one can quantify the phylogenetic diversity of communities, since that topic is covered thoroughly in chapter 3.

Data regarding the demography of individuals and ultimately the temporal dynamics of communities are invaluable for refining our understanding of the mechanisms underlying community assembly and species co-occurrence. This is particularly true when the demographic performance of individuals is known within a spatial context where one can quantify how performance relates to the local abiotic and biotic environment. For example, a classic approach in forest ecology has been to quantify the relative strength of intraspecific negative density dependence via modeling the growth and survival rates of seedlings as it relates to the density of conspecific species in the immediate neighborhood of a focal individual. While intraspecific negative density dependence is nearly always detected for forest trees, an interesting question is whether the identity of neighboring heterospecific species influences the performance of an individual. For example, a heterospecific species in the neighborhood may be a strong competitor if it has similar traits related to resource use or, as is more likely in tree communities where direct seedling competition is often believed to be diffuse (e.g., Paine et al. 2008), a heterospecific species may share similar pests and/or mutualists. It is nontrivial to know this information about all heterospecific species, and this naturally led to not treating neighboring individuals in a binary fashion (i.e., conspecific or heterospecific), but in a more continuous fashion weighting heterospecific species in models by their phylogenetic distance (e.g., Webb et al. 2006; Uriarte et al. 2010; Paine et al. 2011; Lebrija-Trejos et al. 2014). The rationale again was that closely related species may compete more intensely, but also it was and is often based on empirical results demonstrating that pests tend to be shared more frequently between closely related species (e.g., Futuyma and Mitter 1996; Weiblen et al. 2006; Gilbert et al. 2012), such that Janzen–Connell-type effects (Janzen 1970; Connell 1971) may give rise to improved performance in a more phylogenetically diverse neighborhood. A nice early example of research employing this framework came from Webb et al. (2006), which indeed showed that individual seedling performance in

a Bornean rain forest was typically higher when the neighboring individuals were more phylogenetically diverse. Additional work has been done on this topic (Uriarte et al. 2010; Paine et al. 2011; Lebrija-Trejos et al. 2014), including experimental investigations (e.g., Liu et al. 2012), and it seems likely that the phylogenetic signal in pests and the implications of this for the phylogenetic structure of plant community are still an understudied topic.

A second realm of influential research has revolved around the quality of the phylogenetic tree being used for inferences. The software Phylomatic generated by Webb and Donoghue (2005) made phylogenetic analyses in community ecology more feasible, and it removed the old excuse used by many comparative plant ecologists not taking phylogenetic nonindependence into consideration due to a lack of phylogenetic information for their study system. However, the pragmatic solution given by Phylomatic to enable phylogenetic analyses in ecology produced phylogenetic trees with large numbers of polytomies and branch length estimates that were admittedly very rough estimates. As a result, many studies were criticized for using phylogenetic trees produced by Phylomatic, but it was rather unclear how great the impact of uncertainty in a Phylomatic tree was on community phylogenetics. Using simulated data and molecular phylogenies based upon DNA barcode regions, colleagues and I addressed this important methodological issue (Kress et al. 2009; Swenson 2009a; Kress et al. 2010; Pei et al. 2011). While there were subtle variations in the results among studies, the general finding was that Phylomatic trees were biased toward finding random phylogenetic structure in communities. However, in one case we found that the nonrandom results in a well-known study using a Phylomatic phylogeny (Kembel and Hubbell 2006) were actually nonrandom in the completely opposite direction when using a molecular phylogeny (Kress et al. 2009). Our general findings from these works likely will not hold for every possible system, but it was at least encouraging to me that Phylomatic trees were not producing nonrandom results when they should have been random, particularly when this was the time period when community ecology was very deeply entrenched in the niche versus neutral debate. One other important outcome of the work investigating biases due to uncertainty in Phylomatic phylogenies was the recognition that DNA barcodes may be an efficient and feasible approach for estimating community phylogenies, giving them an additional use beyond species identification and ecological forensics (Kress et al. 2009; Swenson 2012a). For example, in tropical tree communities where we previously lacked any kind of sequence information for half of the species, even the most scrutinized regions (e.g., Barro Colorado Island, Panama), and therefore had no hope of building a molecular phylogeny, DNA barcodes allowed us to

produce a community molecular phylogeny containing hundreds of species in a relatively rapid, financially feasible, and reliable manner (Kress et al. 2009). DNA barcodes will never be a perfect solution for building community phylogenies, particularly when there are many congeneric species involved, but they have proven invaluable for helping resolve relationships between genera in communities to produce refined measures of community phylogenetic structure.

4.8. Challenging the Clustering Assumption in Light of "Modern" Coexistence Theory

The use of the phylogenetic proxy to study community assembly and coexistence has generally been plagued with two main criticisms. First, whether closely related species were actually similar was frequently questioned. Second, the phylogenetic trees used were often far from ideal. However, if one was able to infer a relatively reasonable phylogenetic tree and demonstrate phylogenetic signal in a variety of trait or niche axes, there appeared to be few complications. These complications included opposing assembly mechanisms giving rise to random phylogenetic patterns (e.g., Swenson and Enquist 2009) and the impossible-to-solve problem initially raised by Darwin (1859), where we will never know the exact reason why two closely related species don't coexist based upon a phylogenetic pattern alone. In 2010, Mayfield and Levine presented another clear complication for inferring processes from phylogenetic patterns particularly on very local scales and with respect to coexistence theory that takes into account performance and niche differences (Mayfield and Levine 2010). The argument began with a rehashing of the typical inference pathway where if traits or niches have phylogenetic signal, then phylogenetic overdispersion indicates the importance of biotic interactions and phylogenetic clustering indicates the importance of abiotic filtering. Mayfield and Levine (2010) then discussed Chesson's coexistence framework (Chesson 2000), where species with small niche differences may competitively coexist so long as they have small performance differences. In other words, if niches are conserved and closely related species coexist due to small performance differences, then one would get a phylogenetically clustered pattern. Taken to the extreme, one may then be tempted to say that all nonrandom phylogenetic patterns indicate competition and abiotic filtering is relatively unimportant.

There are several potentially important issues raised by the Mayfield and Levine (2010) paper that go beyond a simple conclusion that phylogenetic clustering could mean competition even when traits or niches are conserved.

First, Mayfield and Levine (2010) suggest a broadening of the concept of abiotic filtering and use the term "environmental filtering," which simultaneously encompasses abiotic and biotic interactions. The authors argue, though, that this doesn't allow researchers to tease apart the roles of competition and the abiotic environment, which they state is a general goal of many. This is a valid point generally, but it does appear to draw the conclusion that most community ecologists don't appreciate that both processes are acting at the same time, such that the abiotic environment sets the stage for competition and this feeds back to potentially alter the environment. Thus, Mayfield and Levine (2010) simply are arguing that in those instances where species with similar niches coexist in an environment that constrains the diversity of traits or niches via small performance differences and they are therefore competitively dominant compared to species not able to coexist, we may get a phylogenetically clustered pattern with conserved trait or niche evolution. In such an instance, it may be completely possible that those absent species could theoretically grow in the abiotic setting in the absence of the superior competitor and therefore there is no strict abiotic filtering (*sensu* Kraft et al. 2015). However, it appears clear that in such instances the abiotic environment has played a large role in selecting the phenotypes that are competitively dominant in the system. Thus, a simple solution to this problem is to state that the result could be produced by a strong selection of a small subset of phenotypes by the abiotic environment, which are competitively superior to other phenotypes. This nuanced view is, from my perspective, likely more in line with what most community ecologists had in mind while making their inferences, and I would guess that most would not argue that their inferences regarding the relative importance of the abiotic environment in shaping the phylogenetic or trait structure of assemblages did not mean competition could not or was not happening, and that absent species could not exist in the study system in the absence of other species.

One response to the Mayfield and Levine (2010) work has been to totally embrace the Chesson (2000) approach and to test it experimentally as it relates to phylogenetic distance. At first blush, this appears to be a great idea, and there has been nice recent work on this topic (e.g., Narwani et al. 2013; Godoy et al. 2014). However, tests of the Chesson (2000) framework can only be conducted in a really meaningful way in relatively simple systems on organisms with short life spans, using experiments that are often quite removed from a natural setting.

One last consequence of the Mayfield and Levine (2010) work has been a knee-jerk reaction that all patterns of phylogenetic clustering indicate competition. Competitive outcomes can produce assemblages with similar spe-

cies, particularly in instances where the abiotic environment has a strong selective role. However, one must be careful with how broadly we apply the lessons of Mayfield and Levine (2010). For example, the phylogenetic clustering of southeast Asian tree assemblages relative to South American tree assemblages is best explained by biogeographic history (e.g., Dipterocarpaceae) rather than small performance differences, and the phylogenetic clustering in angiosperms toward the poles is no doubt driven by abiotic filtering and not competition. I do not mean to imply that Mayfield and Levine (2010) do not understand these things, but it is clear that the valid and important point made by Mayfield and Levine has overshot its bounds in many instances already when readers of their work haven't carefully considered the limits to the implications of their work. In sum, the Mayfield and Levine (2010) paper marks an interesting and important contribution to community phylogenetics research, particularly on very small scales, that should provoke researchers to provide a more nuanced set of inferences. However, the future of linking Chesson's coexistence theory with the phylogenetic structure of communities is likely bleak, simply due to the challenges of testing the framework in an interesting and broadly informative way and the sheer difficulty in linking any phylogenetic pattern to any processes irrespective of the framework used. Furthermore, as I stated at the outset of this chapter, coexistence is not community assembly. Rather it is one of the facets of it, and we cannot fully understand community assembly by only investigating local-scale species coexistence. This further argues for a reconsideration of whether phylogenies should still be used in community ecology, and if so, whether we need to fundamentally shift how they are used in order to progress our understanding of the forces underlying community assembly. In the next section, I tackle these exact questions.

4.9. An Outlook on the Future of Community Phylogenetics: Abandonment or Conceptual and Analytical Adjustments?

The clearest limitation of using phylogenetic proxies in co-occurrence and community assembly research is whether or not the assumption itself is valid. Further, even in those cases where the assumption may be valid, coexistence theory researchers working on very local scales have argued that phylogenetic results may still lead one to faulty inferences. Although the accumulation of community phylogenetics papers in the literature seems not to have slowed greatly in the face of these important critiques, there is certainly no doubt that publishing research demonstrating nonrandom phylogenetic structure is very difficult in the more prestigious ecological journals. Thus, it may appear

that community phylogenetics is dying a slow death, and we must ask ourselves whether we should abandon the field altogether or revise the research program by making key conceptual and analytical adjustments.

One may argue that simply scaling out the community phylogenetics research program may mitigate most of the current problems. Specifically, on larger taxonomic scales, the variation in phenotype among closely related species becomes increasingly small in comparison to the total variation among all of the species in the study. Further, as the spatial scale of the study increases, inferences about important biogeographic events becomes possible. I agree that both of these solutions are useful and should be used more frequently than they traditionally have been (e.g., Swenson and Umaña 2014), but these solutions don't completely get to the heart of the troubles with community phylogenetics, and a series of more radical changes may be necessary.

The largest issue with the phylogenetic analysis of coexistence and community assembly is the phylogenetic proxy itself and the general lack of true evolutionary inferences. Scaling out taxonomically in most cases will increase the phylogenetic signal in the data set, but this approach in a sense washes out the variation within terminal clades most closely aligned with diversification and coexistence. Further, one of the most attractive parts of using phylogenetic information in community ecology, at least from my perspective, has always been the potential to truly integrate evolutionary history into community ecology. Indeed, many community phylogenetics articles state that the phylogeny is being used to say something about evolution or evolutionary history when in reality it is not. Rather, we are assuming something about evolution and using that assumption instead of inferring something about evolution and then quantifying its downstream impact on community structure and feedbacks. From this perspective, the integration of evolution and community ecology has been lacking.

I propose that instead of spending additional time worrying about issues with the phylogenetic proxy and how to deal with them, we should be taking two different approaches. First, phylogenetic diversity will always have a place in community ecology as a way to estimate the possibility that unmeasured trait or niche axes that have signal explain the dependent variable. Indeed, we frequently see research in the literature that shows a strong significant phylogenetic pattern and no pattern using the traits measured. We will never know from those studies why the phylogenetic information is a stronger predictor, but it can serve as a potentially informative catchall and an indicator that there is an important trait or niche axis we are not measuring and should track down (Cadotte et al. 2013).

Second, we should spend much more time worrying about why evolutionary history has been so poorly integrated into community ecology despite the enormous number of community ecology researchers now using phylogenies in their work. When we consider this issue deeply and consult lineage-specific investigations in the evolutionary literature, the way forward will likely become much more clear. Specifically, the way forward for phylogenetic investigations of community assembly will be to ultimately abandon the phylogenetic proxy in almost all cases, and to use the phylogeny as a backbone for investigation on which ecological information is hung. Specifically, I am suggesting that phylogenies are and will be most useful in community ecology when we trace biogeographic, trait, and niche data onto the phylogeny to infer their history and quantify the impact of this history on present-day community structure. In this way, one infers an evolutionary history rather than assuming it to explain the same community pattern. This research program may be more challenging and foreign for a community ecologist than community phylogenetics as it stands today, and the key lurking challenges will be: (1) generating robust well-sampled phylogenetic trees for multiple monophyletic focal lineages that co-occur regionally and locally rather than inferring polyphyletic "community phylogenies"; (2) measuring traits more closely and mechanistically linked to performance rather than easily measured traits; (3) and a willingness to embrace that larger-scale processes and events explain more about community structure, dynamics, and diversity globally than the local-scale patterns generally studied in community ecology. None of these challenges are easy to confront, and certainly my own research program using phylogenies in community ecology has generally failed to meet these challenges. However, I do strongly believe this is how phylogenies will need to be integrated into community assembly and coexistence research more frequently going forward, if community phylogenetics is to remain a viable field of research and for it to truly meet the promise of a field that integrates evolution, systematics, functional ecology, and community ecology. In the next chapter, I will discuss lineage-specific research that aligns more closely with what I see as the future of community phylogenetics. I will discuss the historical development of this approach, some influential examples, and a discussion of how and why the approach should be utilized more frequently in the ecological literature.

5

Community Assembly: Phylogenies as a Backbone

In the previous chapter, I outlined the development of a research program that has relied on the use of phylogenetic relatedness as a proxy for species similarity. An optimistic view of the proxy research approach is that acknowledging and quantifying the phylogenetic relatedness of species in a sample provides more information than what can be gleaned from a list of species alone. From this vantage point, we may appreciate the clear flaws with the phylogenetic proxy approach while also acknowledging that knowing some additional information is useful. A less optimistic view of the phylogenetic proxy is that because relatedness is correlated with traits and niches to varying degrees across taxa, locations, and points in time, therefore a phylogenetic approach to community ecology is a waste of time and should be abandoned as an ill-advised fad or bandwagon. Despite the serious drawbacks with using a phylogenetic proxy, I am still of the opinion that knowing something additional about the species in a species list is better than knowing nothing more than their names. Further, dismissing a research approach via name-calling is careless and incurs a potentially large opportunity cost. Specifically, a thoughtful reconsideration of how phylogenetic information could or should be used in community ecology is far more useful than throwing out the idea of phylogenetic community ecology.

This chapter is designed to push community ecologists to reconsider how they are using phylogenetic information in their research. The research path that I will present as a much more interesting, valuable, and viable phylogenetic approach to community ecology is not novel. It has been running in parallel with occasional cross-pollination with the phylogenetic proxy literature for decades. Furthermore, this approach has the ability to make more meaningful inferences regarding the intersection of evolutionary his-

tory, biogeography, and community ecology. Lost in the critiques of the phylogenetic proxy approach that focus on the proxy itself and infer a process from a pattern is one of the more damning critiques of this literature—it has largely failed to fully integrate evolutionary history and community ecology. A component of many, if not most, introduction sections to phylogenetic community ecology articles is that phylogenetic information is allowing the researcher to integrate evolutionary history with community ecology. This "integration" often comes in the form of showing that the relatedness of species is correlated with some variable (e.g., a species co-occurrence score). In some ways, this is interesting and important. It indicates that the millions of years of history leading up to this point have left a strong imprint on the ecological pattern under scrutiny. It also serves as a reminder to ecologists that the historical factors they often ignore may play a role that is as large or larger than the variables on which they focus. However, this integration is still very incomplete and not totally satisfying. We still have learned little to nothing about the evolutionary history of the species under study. In other words, we know evolutionary history is influencing our ecological pattern in some manner, but we don't have a clear picture regarding what that evolutionary history is and why it matters. Without knowing such information, it becomes hard to identify any generalities emerging across taxa and ecosystems, which would greatly help in the formation of a true synthesis between evolution and community ecology.

The goal for phylogenetic community ecology going forward should be, therefore, to strive toward a true integration of evolutionary history and community ecology where useful and interesting inferences regarding both the topics are drawn. If this approach is not adopted, then phylogenetic community ecology will likely fade away, at the cost of abandoning the integration of two major research disciplines in ecology and evolution. In the following, I first define the key differences between what I consider to be two largely independent phylogenetic community ecology literatures—one that uses a phylogeny as a proxy and another that uses it as a backbone onto which data is placed. I then present research questions central to the phylogeny as a backbone research program and why they should be of interest to the modern community ecologists. Finally, I outline practical challenges facing the phylogeny as a backbone approach to phylogenetic community ecology.

5.1. Independent Threads in Phylogenetic Community Ecology

Phylogenetic information and relatedness have been used in community ecology for roughly a century. However, phylogenetic information has been

utilized in two fairly different ways. This has produced two literatures that have converged and diverged through time. At present, the literatures are pretty divergent, and it would be instructive to review these two threads of phylogenetic ecology to find commonalities and to frame why using phylogenies as a backbone piece of information rather than a proxy for similarity is preferred.

As a master's student, I was studying the spatial distribution of hybrid zones and phylogeographic breaks in a lab full of speciation researchers investigating cricket reproduction. During this time, I had become increasingly interested in plant functional ecology and my interest in plant community ecology had reignited. However, the biogeographic and evolutionary focus of my master's work left me susceptible to being interested in how biogeography and evolutionary history impact ecological interactions in communities. It was in this context that I came across the work by Webb (Webb 2000; Webb et al. 2002) when applying to PhD programs. I found the integration of phylogenetic information into community ecology exciting.

The first semester of my PhD I spent trying to figure out existing community phylogenetics tools (e.g., Phylomatic: Webb and Donoghue 2005; Phylocom: Webb et al. 2008) and digging back through the literature on phylogenetic analyses in communities. Some of the work focusing on relatedness as a proxy for ecological similarity (e.g., Elton 1946) aligned nicely with the work of Webb (2000). However, it did not take long for me to realize there was a substantial literature using phylogenies in community ecology that looked nothing like the phylogenetic proxy literature. This other literature was focused on larger spatial scales, biogeographic history, and the evolution of traits and niches. These pieces of information were then used to infer why some species co-occur while others do not. In short, the phylogeny served as the framework or backbone rather than a stand-in for species similarity.

In the following paragraphs in this section, I will trace what I perceive as the shared originals of these two phylogenetic approaches to community ecology and where they have diverged and converged through time. In figure 5.1, I present a phylogenetic reconstruction of the phylogenetic approaches to community ecology. It serves as a rough timeline and it is not comprehensive, but I think it is useful. We begin with Darwin and work our way up to Jaccard and the measurement of taxonomic ratios in assemblages. We covered these developments as well as the null model debates in the 1920s and again in the ~1970s and 1980s in the previous chapter. Up until this time, the literature was largely unified—not necessarily in opinion, but in language and foci. Community assembly at this point was largely a discussion of historical and biogeographic scale processes though discussion regarding the importance

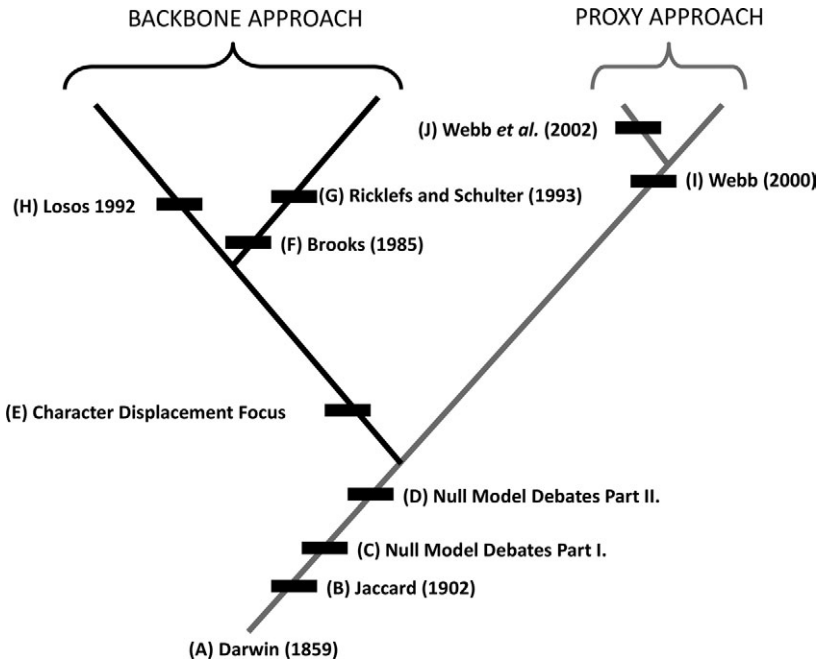


FIGURE 5.1. A phylogenetic tree representing the history of phylogenetic approaches to community ecology. Around the null model debates of the 1970s and 1980s, the lineage diverges into the backbone and proxy approaches contrasted in this book.

of competition permeated throughout. As noted in chapter 4, some of the methodological debates are bookended by Simberloff (1970) and Grant and Abbott (1980), to the point where exhaustion and frustration appear to have taken hold. It appears that at this point that the two phylogenetic community ecology approaches truly began to diverge. One lineage, the proxy and taxonomic ratio approach, lost some momentum but persisted largely in the community ecology literature. However, concerns over null models and the uses of ranks instead of branch lengths limited the literature, and it was not truly revitalized until Webb (2000), along with other works such as Tofts and Silvertown (2000).

The Webb et al. (2002) review and the species issue on phylogenetic community ecology in the journal *Ecology* in 2006 are interesting indicators of the shift in dominance from one type of phylogenetic community ecology to another. This is particularly true when compared to a series of papers published together in *Ecology* in 1996 on the topic of evolution and community ecology. The papers in the 1996 *Ecology* issue represented entirely the phylogeny as a backbone approach to community ecology. Specifically, the

phylogeny was used as a framework on which additional information was hung to infer how the tempo and mode of evolution influences present-day community structure (e.g., Losos 1996). Additionally, some of this work (e.g., McPeek 1996) focused on how present-day ecological interactions feedback to influence community evolution. Note that in none of these papers is the phylogeny used as a proxy for ecological similarity. Ten years later, the *Ecology* special issue was a mixture of the phylogeny as a backbone approach (e.g., Ricklefs 2006) and as a proxy for similarity approach (e.g., Cavender-Bares et al. 2006; Kembel and Hubbell 2006). This distribution of approaches was skewed even more toward the phylogeny as a proxy approach by the time yet another special issue on phylogenies and community ecology was published in *Ecology* in 2012. Indeed, since approximately 2004, almost all phylogenetic community ecology papers have used the proxy approach, with the backbone approach being used infrequently and meaningful evolutionary inferences being few and far between.

As I alluded to earlier, the phylogeny as a backbone approach can be traced back toward the end of the major null model debates in the 1970s and 1980s. At this point, there were several researchers interested in linking the interplay between ecology and evolution, with character displacement often playing an important role in the discussion. For example, the work on the avi-fauna of the Galapagos and character displacement was swept up into the null modeling debates (e.g., Simberloff 1970; Grant and Abbott 1980). Rather than being interested in the relatedness of all species in an assemblage, per se, these researchers were more interested in understanding the evolutionary history of individual lineages. As phylogenies became more readily available and phylogenetic comparative methods took hold, this lineage of research began to diverge into what I consider two subtypes. The first focused on continental scales, the historical assembly of entire floras and faunas, and topics such as codiversification. Note that this work was at times clade-specific or monophyletic, while other work used a phylogenetic framework to infer the importance of historical contingencies that was typically an analysis of a polyphyletic sample of the tree of life, and in some cases the "phylogeny" being used was essentially taxonomic information. Examples of this work are Dan Brooks's work on codiversification of fishes and parasites (e.g., Brooks 1985; Brooks et al. 2006), Farrell's codiversification of angiosperms and beetles (Farrell and Mitter 1990; Farrell 1998), and Ricklefs and Latham's dissection of the north temperate tree flora (Ricklefs and Latham 1992).

The second subtype of the phylogeny as a backbone approach to community assembly was what may be considered the Losos lineage. Specifically, Jonathan Losos's studies of Caribbean *Anolis* ecology and evolution consti-

tuted a uniquely powerful system for phylogenetic community ecology investigations (Losos et al. 1998). Setting this trajectory of research apart is the tractability of the system and a clear focus on the feedbacks between ecological interactions and macroevolution. These feedbacks are frequently not a focal point of the other subtype, where historical processes have a one-way impact on community structure. The work of Losos and colleagues ultimately demonstrated repeated adaptive radiations of lizards following colonization of islands in the Greater Antilles, and the phenotypic divergences of the lizards were related to resource competition.

The work by Rosemary Gillespie provides another powerful example (e.g., Gillespie 2004). She investigated the distribution of ecomorphs among the Hawaiian Islands in the spider genus *Tetragnantha* with respect to their phylogenetic backbone. As with *Anolis*, she found that colonization of a new island was followed by a radiation into a set of ecomorphs that exploited different resources. Thus, in both the *Anolis* and *Tetragnantha* studies, the phylogeny was used as a backbone upon which biogeographic history and phenotypic evolution were traced to draw conclusions regarding the drivers of community assembly (fig. 5.2). This also allowed the researchers to investigate in more detail how ecological interactions have produced the macroevolutionary result. This is the most powerful way in which a phylogeny can be used in community ecology from my perspective.

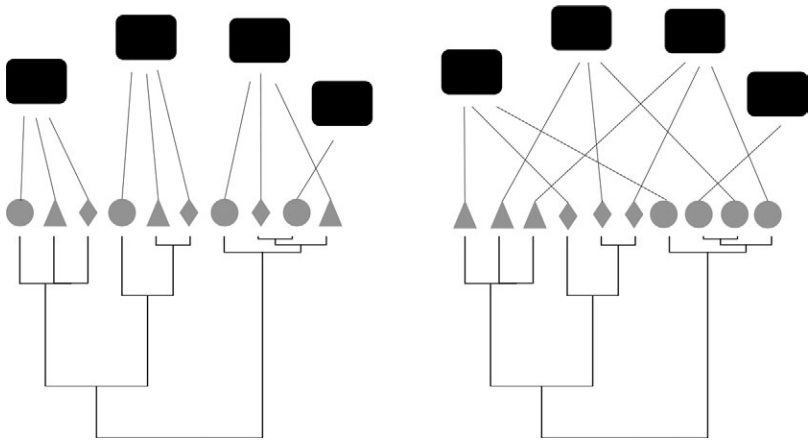


FIGURE 5.2. Alternative hypotheses regarding the historical assembly of island faunas. In both cases here, the islands (black) are composed of functionally diverse communities where functions are represented by different gray shapes. In the example on the left, repeated evolution of traits results in functionally diverse communities on islands. This scenario is in line with the work on *Anolis* (e.g., Losos et al. 1998) and *Tetragnantha* (Gillespie 2004). The example on the right is the assembly of diverse assemblages via dispersal and minimal phenotypic evolution.

From here we can see that two very distinct threads of phylogenetic community ecology have evolved, and the dominance of the backbone approach focusing on evolutionary history has given way to the proxy approach focusing on estimating ecological similarity over the past two decades in the community ecology literature. There have been examples of research that has impacted both literatures. For example, work by Cavender-Bares and colleagues on Floridian plant communities has used both the backbone (Cavender-Bares et al. 2004) and proxy (Cavender-Bares et al. 2006) approach. Combined with the *Ecology* special issues demonstrating both approaches, this highlights that the two lineages of researchers are not unaware of one another. Rather, they have chosen to use phylogenetic information in two very different ways.

The question that now faces those interested in phylogenies and community ecology is: Which approach is the most useful and viable going forward? In the previous chapter, I outlined the severe problems with the proxy approach. In the remainder of this chapter, I will highlight why the backbone approach should be preferred moving forward, and how it will promote the synthesis of community ecology and evolution that is often stated as a major goal behind the use of phylogenies in community ecology. We will begin with reconsidering how phylogenetic information fits into how we, as ecologists, conceptualize community assembly, and how this conceptualization may need to be adjusted. While I would like to push phylogenetic community ecology toward the backbone approach and away from the proxy approach, we should remain cognizant of the limitations of the backbone approach and research challenges that will need to be surmounted to rapidly expand this line of research. Thus, the last several sections of this chapter are devoted to these challenges and how they should be acknowledged or how they may be overcome.

5.2. Phylogenies as Backbones and Modifying the Canonical Framework for Community Assembly

A species pool may loosely be defined as the group of species that could potentially colonize a location. It is fairly easy to highlight the potential flaws in this definition, ranging from the ambiguity regarding the temporal scale on which colonization occurs (e.g., within a lifetime vs. during an interglacial cycle) to new pool members to the practical impossibility of knowing the "normal" dispersal abilities of all species, much less what degree of dispersal is possible during rare events (Lessard et al. 2012). Further, while ecologists have idealized approaches for how one should operationally define a species pool

for their study, these approaches are frequently not possible—particularly for those not working with groups where geographic distributions may be available on many spatial scales (i.e., vertebrates). In reality, species pools are constructed from the list of the species in a small region or a meta-community. Such species pools almost assuredly do not include species that could potentially colonize the study location or communities being studied. Given the above, it may seem surprising that species pools are nearly essential conceptual and analytical tools for ecologists interested in studying community assembly. Assembly necessitates that species come from some source, and null modeling analyses that are foundational to studying community assembly require a species pool (Simberloff 1970; Colwell and Winkler 1984).

A stereotypical conceptual diagram for community assembly typically has a species pool that is sorted somehow into increasingly smaller groups of species, ultimately ending with the local assemblage of species (fig. 5.3; Weiher and Keddy 1995; Lambers et al. 1998; Weiher and Keddy 2001). Some have modified this flow diagram, somewhat, to include the possibility that local species interactions modify the abiotic environment or species interactions within regions, but these feedbacks do not make it back to the species pool scale (fig. 5.4; HilleRisLambers et al. 2012). Thus, the process of community assembly is conceptualized, purposefully or not, as a largely unidirectional phenomenon. For example, there are no inputs into the species pool itself, indicating that it is just a given entity. Is this to indicate that we do not care what processes explain the composition and diversity of the species pool itself? Do the lack of feedbacks between scales on the diagram indicate that we do not think contemporary ecological interactions will alter the future species composition at regional scales? I am sure that the vast majority of community ecologists would say we should be interested in the macroevolutionary processes influencing species pool composition and diversity and ecoevolu-

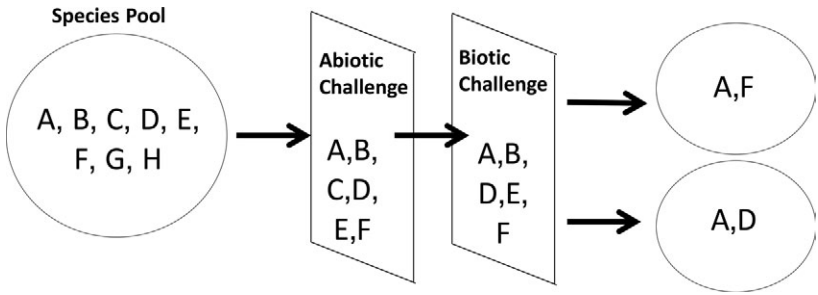


FIGURE 5.3. The canonical schematic for community assembly where a species pool is filtered through the abiotic and biotic environments successively until local communities result.

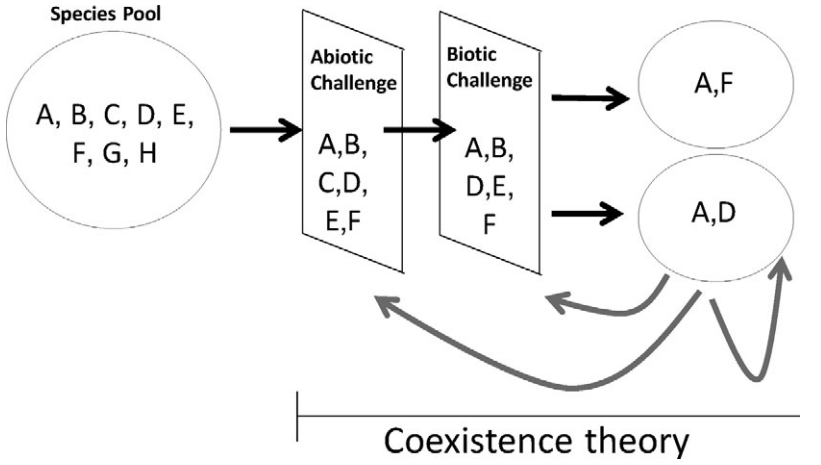


FIGURE 5.4. A more up-to-date twist on the canonical community assembly schematic as outlined by HilleRisLambers et al. (2012). Here, feedbacks between local communities and the abiotic and biotic environment are included. Note that there is still no consideration of how the species pool was formed in the first place and no consideration of how ecological interactions influence the pool.

tionary feedbacks. They may think such investigations are for evolutionary biologists to study, but this only highlights a disinterest in an integration of evolutionary history into community ecology. I would also argue that the diagram clearly outlines the priority placed by those studying community assembly on understanding species composition on very local scales as an endpoint and an unwarranted belief that differential macroevolutionary rates and their impact on species pool composition and diversity are not a major influence on community assembly.

Here, I propose that we must alter our classic community assembly diagram to provide some more biological realism and to broaden our thinking of the processes that should be of interest to those studying community assembly (fig. 5.5). While phylogenetic analyses are not well suited for addressing all of the processes and questions that arise from the modified community assembly diagram, they are useful for addressing questions regarding the processes responsible for generating the composition and diversity of species pools. I will use the diagram proposed by HilleRisLambers et al. (2012), which is used by many as the canonical community assembly diagram inclusive of coexistence theory. It is important to note that stable coexistence is not a necessary component of community assembly, and if it does play a major role, at least in tree communities, it is due to large niche differences driven by strong intraspecific negative density dependence and relatively very weak pairwise interspecific competition.

The first simple modifications we can make to the canonical community assembly diagram are feedbacks between the subregional scales and the species pool. These feedbacks recognize that ecological interactions govern microevolutionary and macroevolutionary outcomes that influence species pool composition and diversity. The net diversification rates that influence species pool properties do not simply just occur, and everything that follows is a unidirectional flow to communities and coexistence theory. Ecological interactions largely determine the demographic success of individuals and therefore population persistence, which is necessary for species formation and a reduced probability of extinction. A second modification to the canonical diagram is the addition of biogeographic history and the associated ecological feedbacks. This is to simply recognize that dispersal, vicariance, and biogeographic happenstance all contribute to species pools. Most ecologists can quickly point to instances where species pools are strongly impacted by biogeographic legacies and events. The feedbacks recognize that while dispersal events happen, for example, population persistence is necessary for the event to have an impact on species pool composition. The modifications I have proposed do not include processes that should be foreign to any community ecologist. However, they are not easy to study, and in some instances can almost be impossible to predict (e.g., rare dispersal events), but this is not reason enough for their omission from our conceptual framework for

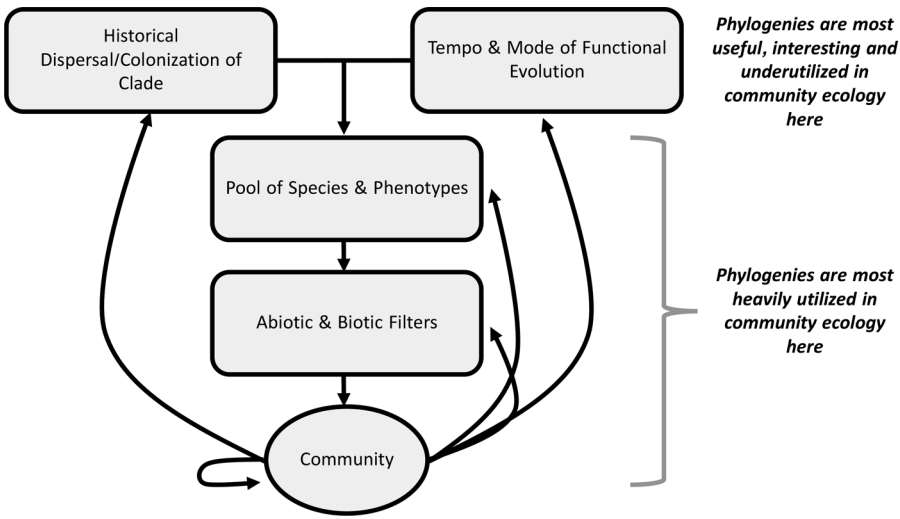


FIGURE 5.5. The proposed remodeling of community assembly where there are multiple feedbacks, including feedbacks into the processes that impact species pool composition and diversity. Additionally, there is a focus on the mechanisms influencing pools and the suggestion that phylogenies are best used for these questions and less useful for questions regarding the filtering of pools to local communities.

community assembly. Continued omission will serve to slow advancement of knowledge.

Now that we have modified the canonical conceptual framework for community assembly to include the processes impacting species pool composition, we can proceed to asking how phylogenetic information is best used in this framework. The phylogenies as a proxy for ecological similarity approach that was described in detail in the previous chapter has been used extensively on the subregional scales in our community assembly framework. I have outlined the significant problems with this approach and why it should be abandoned in most cases. Phylogenetic information, however, still has a role to play in the community assembly framework. Specifically, the phylogenies as a backbone approach to community ecology is well suited to addressing questions at the regional to global scales, where the processes influencing species pool composition and diversity are the primary focus.

The first way that the phylogenies as a backbone approach can assist in helping us understand species pool composition and diversity is through the reconstruction of geographic distributions through time and net diversification. The reconstruction of geographic distributions is a common output from most phylogenetic systematics work. This may be an inference of the number and directionality of dispersal events or an inference of vicariance and may, therefore, be considered just the documentation of history, but species pool composition and community assembly cannot be understood without it. The reconstruction of geographic distributions also allows one to quantify rates of net diversification within and across regions, which is also fundamental to understanding community assembly. Is the diversity of the species pool in the region primarily due to many dispersal events or positive net diversification in the region, and how is this ultimately related to the number of species that locally co-occur or regionally partition habitats? Next, by tracing trait and niche evolution onto the phylogenetic backbone, the researcher can really begin to weave together the tapestry of ecological interactions and evolutionary processes and how they influence species pool composition and diversity as well as local-scale patterns of co-occurrence and community dynamics. For example, one could document that net diversification plays a larger role in determining species pool diversity in one region versus another, and then ask whether rates of phenotypic evolution are similarly elevated, and where this increased phenotypic diversity permeates to local scale due to niche partitioning or is realized at the regional scale, where different phenotypes are partitioning a greater variety of habitats or perhaps partitioning habitats more finely. As this point, the researcher is able to traverse the scales and consider the potential feedbacks in the modified

conceptual framework for community assembly. Importantly, the phylogeny is no longer being used as a proxy for ecology, and it is entirely being used to help reconstruct historical events, rates of net diversification, and the associated tempo and mode of trait or niche evolution. Just as importantly, using the phylogeny in this way does not solve all problems in the community assembly research program. It does not help elucidate how local-scale interactions influence community structure and dynamics. Additionally, it would be difficult to produce convincing inferences regarding ecoevolutionary feedbacks from this information alone. Thus, a comprehensive research program still has a major component that one might think of as traditional ecology and a major evolutionary ecology component. It therefore becomes clear that the problem of community assembly is not an ecological problem or an evolutionary problem; it is a problem that requires the synthesis of many pieces of information and fields of research. From my perspective, this makes community assembly one of the most fascinating, challenging, and interesting fields of study.

5.3. Major Questions Driving the Backbone Approach

In the previous section, I outlined some questions one may begin to ask regarding community assembly once a phylogeny as a backbone approach is embraced. Here, I will elaborate on these questions in the hope of focusing the trajectory of research in this field. Many of these questions or research objectives have long been on the mind of community assembly researchers, but I would argue that most have not addressed them adequately or convincingly, and this is certainly the case if the phylogeny was used in the study as a proxy for ecological similarity.

The first major question is the degree to which lineage diversification in a region versus dispersal to a region or vicariance has impacted species pool composition and diversity, and how this is or is not eventually realized at the local scale. The most well-known and fascinating investigations into this question are based in insular systems, and often find that within-region diversification plays a dominant, and often predictable, role. However, noninsular systems may behave quite differently, and addressing this possibility is one of the first major questions that could be quickly answered with a backbone approach. There are, of course, many pieces of information that cannot be gleaned from this investigation alone. For example, what the putative drivers of these outcomes were and how those drivers may help us understand the ecological interactions determining current community dynamics would be left unanswered.

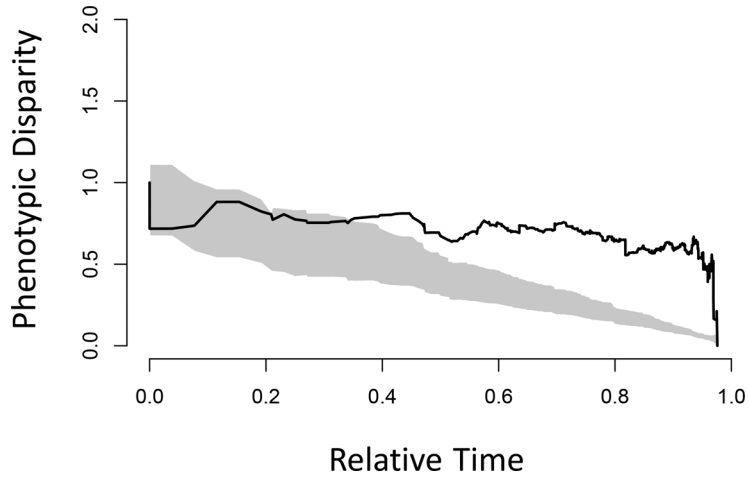


FIGURE 5.6. A hypothetical disparity through time plot (Harmon et al. 2003). Here, the black line indicates the phenotypic disparity between the daughter lineages from a node running from the root (left on *x*-axis) to the tips (right on *x*-axis). The gray shading represents a null distribution generated by simulating traits via Brownian motion on the phylogeny 999 times and calculating disparities at each node of each simulation.

Next, what is the tempo and mode of trait or niche axis evolution, how does this vary among traits or niche axes, and how is this related to lineage diversification and local-scale co-occurrence? This, of course, is not simply one question and is not easily answered, but the questions are intertwined and are best discussed as a major overall objective. Tracing the tempo and mode of trait evolution can be accomplished simply enough with methods such as disparity through time analyses (Harmon et al. 2003; fig. 5.6). Such analyses could be coupled with more detailed analyses of clade-specific trait diversification as it relates to the biogeographic history of the clade. Does trait diversification coincide with dispersal and colonization of new regions, presumably in response to a novel environmental setting, or does it occur between lineages within a region, presumably promoting their co-occurrence? If it is the second situation, is co-occurrence promoted by habitat partitioning on larger scales within the region, or do the lineages also locally co-occur promoted by their niche differences? Woven into all of this, ideally, would be a consideration of how the processes differ among trait axes and what that can tell us about the ecological interactions driving geographic distributions and ultimately community structure and dynamics.

A final line of investigation that I will suggest should be explored with more frequency is linking the rates of historical encounters between sister lineages, their present-day levels of local co-occurrence, and trait evolution

(e.g., Sedio et al. 2013). For example, one can identify the instances where sister species presently co-occur. The co-occurrence, here, could and probably should be quantified on multiple spatial scales. Next, it would be informative to infer the extent of historical encounters or range overlap. Have the sisters been historically isolated and only recently come into secondary contact? If so, do they manage to co-occur on only regional scales due to habitat partitioning or via a tension zone, or do they also manage to co-occur locally, perhaps facilitated by trait divergence while in allopatry, thereby promoting niche differences? In answering questions such as these, a researcher would be synthesizing concepts, theories, and analytical approaches from speciation to biogeography to coexistence theory. Clearly, one would not be able to provide the final word on any one of these particular topics from just this one study design, but it would provide a broader and more synthetic picture of the study system than a typical study could ever hope to provide. One example of research closely aligned to this research trajectory comes from work on ovenbirds by Tobias et al. (2014). Their work did not investigate the historical overlap of species ranges, but rather compared present-day sympatry or allopatry (defined in a binary fashion). They show that sympatric pairs do, indeed, have higher trait divergences than allopatric pairs. The analyses were done using all pairs, but analyses of sister pairs found consistent results. The research team also showed that the trait divergence in sympatry result was related to time since divergence, where sympatric species on average have been diverged for longer periods of time. Combined, the results showed that trait divergences are perhaps more related to time than present-day co-occurrence, per se, and that, if anything, some traits such as birdsong converge with enough time between sympatric pairs (Tobias et al. 2014). These are interesting results, and the analytical framework is very well conceived. However, the work does point to one of the main challenges of conducting work scaling from macroevolution to present-day community structure and distributions. That is, making causal statements regarding time since divergence, co-occurrence, and trait divergence is very difficult. In the ovenbird work, the authors, in a sense, attempted to control for time and stated that there was nothing spectacular in the end regarding trait divergences between allopatric and sympatric pairs. However, one could easily take the alternative view that it simply takes a long time to evolve trait differences, that these are likely done in allopatry, and that eventually these species are able to co-occur due to these built-up differences. These are not easy puzzles to solve, and likely cannot ever be totally solved, due to their historical nature. Additionally, I am not highlighting this issue to state that Tobias et al. (2014) have done anything wrong. Rather, I am simply pointing out the complexity of trying to

disentangle systems that have been running their course for millions of years. Attempting to address such synthetic questions is exciting, and nothing we should avoid due to these difficulties.

5.4. Phylofloristics and Phylofaunistics

A few years back, Natalia Umaña and I introduced a potential field of research that we called phylofloristics (Swenson and Umaña 2014). Phylofloristics is defined as the use of phylogenetic information to reconstruct the similarities and historical assembly of entire floras. While I have not seen the term "phylofaunistics" used in the literature, we could define it similarly. Floristic and faunistic studies have always had a phylogenetic aspect to them through comparison of generic and familial composition as well as character similarity, so it is worthwhile to make it clear how phylofloristics is actually anything different. The key difference I was trying to point out is that it is now becoming possible to build trees containing many to most species in floras or faunas, and to use time-scaled phylogenies (i.e., chronograms) to inform the analyses. The benefits of such information would be the ability to resolve the dispersal histories of lineages to the point where the timing of the assembly of the flora or the fauna of an entire region would be possible.

At present, most groups don't have phylogenies of the quality that would allow for highly detailed analyses of the assembly of entire floras or faunas. The main exceptions may be birds and mammals, but the quality of the large-scale and well-sampled phylogenies for these groups that are available are not uniformly appreciated. Other possibilities might be insular floras and faunas that have been studied extensively (e.g., Hawai'i; Ree and Smith 2008), but the phylogenetic relationships between species in these systems and the lack of sampling of related species in other parts of the world make it unlikely that these systems are currently feasible for a detailed phylofloristic or phylofaunistic study.

Given the limitations of currently available data, many of the most interesting phylofloristic and phylofaunistic studies are in our future. I expect that the first impactful analyses will be those simply restricting the dispersal history of lineages and the timing of diversification. In some instances, such work has been accomplished by comparing phylogenetic inferences for multiple genera or families (e.g., Donoghue and Smith 2004). This approach is grounded firmly in the realm of systematics and should serve as one major trajectory to follow in the future. Studies that are conducted in regions with few major lineages and dispersal events may be fairly tractable, and likely will not lead to the invention of novel methods or approaches.

As phylofloristics and phylofaunistics scales out to use larger phylogenies (e.g., a global-scale study) and to consider diverse regions with many diverse lineages (e.g., the tropics), new analytical approaches may need to be developed or novel combinations of existing methods may be needed. Here, I suggest one way in which existing methods may be combined to elucidate previously obscure phylogenetic connections between floras or faunas. The approach starts simply, with conducting a measurement of the phylogenetic beta diversity between the regions being compared. This dissimilarity can then be used to cluster regions based on their similarity. A phylofloristic study could end at this point as a description of overall similarity between regions, and this is what we did in our original phylofloristic study (Swenson and Umaña 2014). This approach, while a valid starting point, has serious limitations. The most obvious limitation is that we do not know why two regions are more similar to one another than a third region. Correlative analyses of biogeographic and climatic factors could be utilized for this purpose (Swenson and Umaña 2013), but what aspects of the phylogeny are shared would remain unclear. In other words, the lineage overlaps that are the main drivers of the statistical pattern are unknown.

One approach to resolving this problem is simply quantifying the percent overlap in a given taxonomic rank (e.g., what genera and families are shared). However, deeper phylogenetic relationships are ignored under this approach, and these basal nodes are likely to be frequently important, as larger and larger phylogenies and global-scale analyses are attempted. A simple set of analyses might help resolve this issue. The first would be to simply quantify whether the tips from every internal node in a phylogeny are overrepresented in a given region. For example, one would quantify that 15 of the 20 species in a clade are found in a region, and then compare this to the number of species that should be expected to occur in the region given the size of the clade and the species richness of the region. This could be done using a null model, where one would randomize the names of species across the tips of the phylogeny. A faster alternative would be to analytically solve the probability by using a hypergeometric probability distribution.

Next, one would compare the results from each internal node across the regions and extract the nodes that are significantly overrepresented in both regions. These nodes would represent the major drivers of the phylofloristic or phylofaunistic connections between two regions. Once these nodes are identified for all region pairs, their estimated ages and the ecological characteristics of the subtended species can be compared between the regions to gain further insights into why these regions are similar and whether they represent a convergence or not.

What I have presented here are two initial types of phylofloristic or phylofaunistic analyses. The approaches could be used to begin to reconstruct the assembly of entire floras and faunas, which is a major component of community assembly. The approaches are, however, not highly similar to the phylogeny as a backbone approach to community ecology I have outlined previously in this chapter. They do avoid the proxy approach and focus on historical inferences, which is why I have discussed them here, and I think the diversity and quality of the analyses made in this realm will increase rapidly in the near future as the size and quality of phylogenetic trees continues to increase.

5.5. Challenges: Equivocal Inferences

In the text leading up to this point in the chapter, I have attempted to highlight the insights and advances that can be made toward a more holistic understanding of community assembly that can be gained by using the phylogeny as a backbone for study rather than a proxy. In so doing, I have skipped past several key challenges and problems with the backbone approach that I will highlight in the next several sections.

The first challenge I will note, which is obvious to phylogenetically inclined researchers, is that tracing anything onto a phylogeny (e.g., geographic history, trait evolution and ancestral stages, ages) often results in large levels of uncertainty (Losos 2011). For example, the age estimate of an internal node may have a plus/minus of 10 million years. Depending on your outlook, this may not be a major issue, but if one is trying to reconstruct the timing of floristic or faunistic assembly, this could be a major issue. Additionally, error will be compounded across clades and sources of data to the point that it might be hard to make any reasonable inferences with respect to important hypotheses too deep into the phylogeny. Thus, the researcher will need a clear-eyed and sober approach to their data and results, realizing their limitations throughout the investigation (Losos 2011).

5.6. Challenges: Building Taxonomically Well-Sampled Phylogenies for Community Analyses

The second major challenge for the backbone approach is a requirement for dense taxonomic sampling in the phylogenetic trees being utilized. This is challenging because the assemblage of species that an ecologist encounters locally is typically composed of tens to hundreds of genera from tens to hundreds of families. For example, in two of the best-studied tropical tree communities in the Neotropics, Barro Colorado Island (BCI), Panama, and

Luquillo, Puerto Rico, most genera are represented by one to a handful of species. Certain genera such as *Psychotria* and *Inga* may be particularly diverse in the BCI forest, with around 10 species co-occurring, but these genera contain nearly 2,000 and 300 species (Kress et al. 2009), respectively. In other words, the taxonomical sampling of these genera from these localities is still quite sparse. This sparse sampling would be less of a problem if the species in a locality formed a monophyletic group (e.g., Caribbean *Anolis*), but they generally do not in ecological studies—particularly in noninsular systems. Thus, tracing the evolutionary history of traits or niches onto phylogenies for these locally diverse genera will likely be misleading, and a broader sampling will be necessary.

The potential solutions to this challenge include focusing on insular systems where diverse assemblages of congeners occur, emanating from a recent diversification that can be sampled on a manageable spatial scale. A downside of this is that it would further bias the literature toward islands, leaving it unclear whether the results generalize to mainland systems that are more diverse and likely have a more complex history of range dynamics. Additionally, many systems will be relatively recently diverged, making phylogenetic reconstruction exceedingly difficult.

A second solution is to focus on vastly broadening the spatial extent of the sampling. On the mainland, regionally diverse genera are also locally diverse. Thus, a trade-off is imposed because high local diversity makes them more interesting for investigations into species interactions and community assembly, but high regional diversity makes the spatial scope of sampling increase to continental or global extents. In the best of cases, museum and herbaria specimens where DNA and morphological measurements can be obtained may make such sampling possible, but this will not always be the case, and additional exploration and sampling will be needed. In either case, such taxonomically focused studies with global scope are likely best carried out in collaboration with a systematist focusing on the group and international partnerships.

5.7. Challenges: Generating Reasonable Estimates of Species Distributions

A second challenge in the phylogeny as a backbone approach is sparse spatial sampling of species distributions, past and present. In some cases, such as vertebrates and north temperate zone taxa, reasonable and detailed range maps of species have been produced and are likely in a digital format. However, for less glamorous groups and in the tropics, our knowledge of species distributions is often poor. While tracing the evolutionary history of traits and niches on phylogenies is, in itself, of interest to an ecologist, ideally, we

would like to know how those traits are related to climate and the geographic overlap (or lack thereof) between related species. Furthermore, knowledge of the biogeographic history of lineages is essential for understanding community assembly and this knowledge cannot be obtained without knowing the distribution of species past and present.

A widely used solution to this problem in ecology and evolutionary biology is the inference of past and present species distributions using ecological niche models (Elith and Leathwick 2009). These models correlate known occurrences and sometimes absences with abiotic environmental data and project the model onto an array of map layers to predict the probability of species occurrence. These methods can be very alluring as they are frequently very easy to implement and produce detailed maps, which may convey to some (falsely) a high degree of certainty. Ecological niche models have been utilized in the ecological and evolutionary literature for over a decade and, in some instances, they are now being used to predict the distributions of tens of thousands of species as a precursor to more detailed ecological analyses. These models, however, have several easily identifiable and potentially serious problems. First, they typically omit any information regarding species interactions, which likely play a not insignificant role in determining the distributions of species. Second, in cases where hindcasting is being performed, they assume present-day constraints on species distributions are the same as those in the past. Further, they are only as good as the data they are supplied, making them susceptible to major errors due to errors in geo-referencing, the spatial sampling, and species identification. These are only some of the major issues that face ecological niche models. That said, beyond major sampling campaigns, which are difficult to fund, such models are the most pragmatic approach forward. However, a researcher should remain skeptical of such projections and detailed scrutiny of the maps is advised prior to use rather than blindly using large collections niche model projections to infer the processes governing the distribution of biodiversity past, present, and future.

5.8. Challenges: Measuring More Informative Traits

A third challenge with the phylogeny as a backbone approach also concerns scale, but focus as well. Phylogenetic ecology has frequently intertwined with trait-based ecology, and for good reason. Ultimately, one major goal is to determine how the evolutionary history of traits impacts present-day ecological outcomes. To accomplish this goal, we must identify those traits that determine ecological outcomes. Functional traits, by most definitions, are such traits (Swenson 2013). However, the functional traits measured by

ecologists are usually very limited. This is particularly true in plant ecology, where a core set of ~10 or fewer traits are typically measured. These traits are presumed to be the key axes of plant functional differentiation and tradeoffs. While these traits are likely to be important, they are often only weakly correlated with demographic rates (Poorter et al. 2008; Wright et al. 2010; Paine et al. 2015; Yang et al. 2018). Thus, there are likely multiple unexplored phenotypic dimensions that are as important or more important than what is captured by a small set of functional traits. For example, plant defense traits are rarely quantified or crudely quantified, as are the dynamic functional responses of plants to important environmental drivers (e.g., drought; Swenson, Iida, et al. 2017). Phylogenetic ecologists must, therefore, continue to push the boundaries and not only trace the evolution of easily measured traits on phylogenies. They should also explore the evolutionary history of less frequently measured traits that are more related to demographic outcomes and species interactions for the phylogeny as a backbone approach to truly advance ecological understanding.

As with taxonomically and spatially sparse data sets, the present challenge requires a substantial increase in data collection efforts. Indeed, quantifying more traits and the "right traits" is perhaps the most difficult challenge to surmount. This is because the ecologist must first demonstrate the ecological relevance of a trait, which itself may take years of work. Second, this trait must be measured across the clade of interest. In many instances, the trait may not be easily measured on museum or herbarium specimens, and traits measured on living accessions may not represent the trait values expressed in natural ecological contexts. Finally, the traits most relevant to species performance and distributions along environmental gradients will not be consistent across species, such that there likely will not be a single trait that describes all ecological outcomes in a clade. Ultimately, this demands a standardized and detailed assay of organismal morphology and physiology that on a regional or global scale goes beyond what is typically measured in the field or on preserved specimens.

An alternative to identifying and measuring the right traits is to quantify species niches and array them onto phylogenetic trees. While this can be done in convincing fashion, such examples typically come from systems where the functional biology and ecological interactions have been well documented. Less convincing will be those instances where species occurrences are related to climatic maps to infer niches. Such approaches serve as an interesting starting point, as do easily measured functional traits, but just like easily measured functional traits, niches defined in this way likely miss important information that actually delimits species distributions (Swenson

2013). Thus, plotting species niches on a phylogeny may appear easier than measuring traits, but it has the same pitfalls and convincing and detailed studies of niche evolution are rare.

5.9. Challenges: Mainland and Not Only Islands

The best work that has been done on community assembly using phylogenies as a backbone has come from insular systems or insular-like systems (Brooks 1985; Losos et al. 1998; Gillespie 2004). There are several good reasons for this. Islands are spatially discrete through time, in many cases, which greatly simplifies inferences pertaining to dispersal events and their timing. Furthermore, islands have greatly reduced numbers of species, and in many cases a single group can constitute a major proportion of the community or even occupy a trophic level all by itself. The mainland, however, is messy. The geographic histories of lineages are difficult to reconstruct, making inferences regarding the importance of dispersal and vicariance and reconstructions of the ecological interactions experienced by a lineage at any point in time less clear. It also makes detailed taxonomic, spatial, and trait sampling even more challenging. However, the majority of the biodiversity in the world does not occur on islands, and it may be reasonable to expect that, while fascinating, the mechanisms underlying community assembly on islands do not play as prominent a role on the mainland. For example, repeated dispersal events followed by niche diversification where all derived lineages coexist is unlikely to occur on the mainland, where ranges contract and expand much more easily and the complexity and variation in the abiotic and biotic milieu across a species range is far greater. Thus, it is critical that phylogenetic investigations into community assembly that use the phylogeny as a backbone are not only conducted on insular systems moving forward. Ideally, such investigations could focus on groups that are insular and mainland, such that clear comparisons can be made regarding the relative importance of different mechanisms. In sum, islands will remain the locations where the most tractable analyses are possible, but messier mainland systems need greater focus to achieve a greater and more holistic sense of what are general properties within or across insular and mainland systems and what is idiosyncratic.

5.10. Challenges: A Full Embrace of the Importance of Biogeography and Evolution for Community Ecology

A final challenge to the phylogeny as a backbone approach to studying community assembly is convincing ecologists to fully embrace biogeographic and

evolutionary history in their research programs (Ricklefs 1987). Despite some progress, the literature on community assembly is still often recalcitrant when it comes to accepting that community assembly is heavily influenced by processes operating over large spatial and long temporal scales. Accepting this does not mean one must disregard the importance of species interactions and, therefore, ecology. Ecological interactions, of course, determine the demographic success of individuals and populations, which is, of course, fundamental to the micro- and macroevolutionary processes that drive species pool composition. In some regions, net diversification rates are elevated, and whether this is the result of stronger biotic interactions or simply more biogeographic opportunity (e.g., geographic barriers) is an area of ongoing debate and investigation. However, I don't think it would be controversial to state that, in either case, ecological interactions are fundamental for population persistence and therefore, ultimately, diversification. Similarly, it should not be terribly controversial to recognize that regions with more species tend to contain local assemblages with more species. Regions with similar environments do not saturate at similar levels of species richness, and this does not mean ecological interactions are unimportant for community assembly and diversity. In sum, in order to move forward and to have a firm understanding of community assembly as a process operating across a broad range of spatial and temporal scales, community ecologists will have to come to terms with the reality that recognition of the importance of biogeographic and evolutionary processes does not need to come at the cost of recognizing the importance of ecological interactions.

6

Global Patterns of Biodiversity, Diversification, Conservatism, and Priority

This volume, up until this point, has focused on the use of phylogenies in ecology for the purposes of species comparisons and community ecology. These were the main foci of phylogenetic ecology until relatively recently. However, the use of phylogenies in ecology has become more varied in recent years, with phylogenetic information permeating almost all aspects of ecology. In this chapter, I will focus on the integration of phylogenetic information into larger-scale ecology that typically focuses on the diversity and composition of large areas and across large gradients. Some of this inevitably overlaps with community assembly, but most of it is distinct enough for it to be discussed independently.

We will begin with a discussion of the hypothesized role of phylogenetic niche conservatism and the latitudinal gradient as well as the cradle versus museum dichotomy regarding the origins of tropical diversity. Finally, I will discuss priority effects, ecological opportunity, and how phylogenetic information may be used in these contexts to understand the evolution of assemblages and biodiversity. Ideally, I would like the reader to take away from this chapter that phylogenies have a place in ecology beyond comparative methods and community ecology, and that they provide a fundamentally important framework for many of the major pressing questions facing ecology.

6.1. Phylogenetic Niche Conservatism and Diversity Gradients

Macroecology began as a field examining emergent ecological patterns found repeatedly across study systems. The drivers of relative abundance distributions, range size distributions, range size-abundance relationships, and allometry were the main cornerstones of macroecology (Brown and Mauer

1989; Brown 1995). Statistical models are central to all of this work, and the consideration of phylogenetic information, for the most part, in early macroecology was with respect to phylogenetic autocorrelation and comparative analyses (Elgar and Harvey 1987; Pagel and Harvey 1988; Ackerly and Donoghue 1998; Symonds and Elgar 2002). Just as in other areas of ecology, this often meant that macroecologists bemoaned the mention of the word "phylogeny" and considered it more of a nuisance than something that should be studied in its own right.

Macroecology, for better or worse, has transformed dramatically over the past decade. The statistical modeling of emergent phenomena is still present, but has largely become overshadowed by a number of other research trajectories not quite adhering to what macroecology was initially conceptualized to be as a discipline. A focus on emergent patterns still occurs in most cases, but frequently the result is a correlative study of every available variable with the pattern. Phylogenetic information is often used in this new spin on macroecology as simply another measure of biodiversity. For example, there are an increasing number of studies simply correlating phylogenetic diversity with a series of abiotic variables (e.g., Safi et al. 2011; Thuiller et al. 2011; Fritz and Rahbek 2012). In other instances, the phylogeny plays a central role as a backbone of conceptual and analytical piece of information. This is particularly true when it comes to the gradients in species diversity and the role of phylogenetic niche conservatism.

A long-running hypothesis in ecology and evolutionary biology is that the environments at lower latitudes and elevations are more climatically benign (Dobzhansky 1950; Fischer 1960), and that this results in stronger biotic interactions that have resulted in more net diversification. Conversely, relatively harsh high elevations or latitudes have precluded the invasion of new lineages and the importance of specialized biotic interactions that would increase net diversification (e.g., Ehrlich and Raven 1964). In 2004, John Wiens and Michael Donoghue formalized this hypothesis in a phylogenetic context explicitly outlining how phylogenetic niche conservatism explains why few lineages have colonized high latitudes (Wiens and Donoghue 2004). Specifically, the difficulty of evolving traits necessary for success in these latitudes (e.g., freezing tolerance) from ancestral tropical lineages created a diversity gradient. Furthermore, this mechanism would result in younger clades, on average, in the temperate zone than in the tropics (fig. 6.1). For example, one might expect families or genera, on average, to be younger in the temperate zone than in the tropics.

The expected pattern of clade age versus latitude has been quantified many times at this point, generally showing older, on average, families or genera

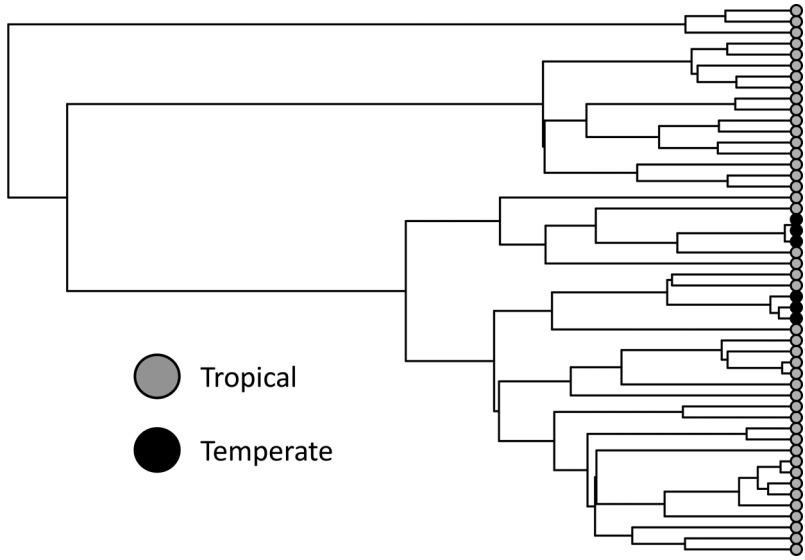


FIGURE 6.1. An example of phylogenetic niche conservatism as it relates to the latitudinal gradient. Here, temperate species (black) have arisen from a few relatively young radiations. Thus, on average, temperate species would be much younger than tropical (gray) species. Note, however, that there are some young tropical species. Also note that the temperate species are clustered into a few clades.

occurring in the tropics relative to the temperate zone. In some instances, the reverse is found with older lineages in the temperate zone (Hawkins et al. 2006; Svenning et al. 2008; Hawkins et al. 2011; Qian et al. 2013; Kennedy et al. 2014). These include gymnosperms in North America and herbaceous plant family ages (Hawkins et al. 2011). However, these exceptions may prove the general rule of niche conservatism such that the ancestral state was more temperate and the derived state of being tropical or subtropical was difficult to achieve. However, this inference would need to be supported with additional information showing that these groups had not simply been pushed out of the warmer regions. For example, the gymnosperms were pushed out by angiosperms as they began to diversify and dominate the planet.

The clade age–diversity relationship has also been tested along elevational gradients by Qian and colleagues focusing on plants (Qian 2014; Qian and Ricklefs 2016). They find that clades tend to be older at high elevations in the tropics, which appears to contradict the niche conservatism hypothesis. Qian and Ricklefs (2016) suggest that these results reflect the evolutionary convergence of tropical lineages invading cold environments independently. Measures of phylogenetic beta diversity would be useful in supporting these claims to demonstrate high turnover of lineages between areas, as would be expected with convergence. However, low turnover might also indicate

convergence if several lineages were located in each cold region (e.g., phylogenetic overdispersion with an alpha diversity metric), but still, neither of these patterns could definitively rule out that these lineages have simply been pushed up the mountain as other lineages have diversified and dominated. In other work by Graham and colleagues (Graham et al. 2009), hummingbird communities along elevational gradients have been shown to be increasingly phylogenetically clustered with elevation, which may be consistent with niche conservatism and environmental filtering. Furthermore, they also report low phylogenetic beta diversity, despite high species beta diversity, between communities on different sides of the Andes (fig. 6.2), perhaps further indicating the importance of niche conservatism, as the results are similar to perhaps one of the most classic papers on niche conservatism by Peterson et al. (1999). Thus, the work from elevation gradients is not as consistent across taxa as it is with latitude, and more information is needed to reconcile the elevation patterns with the latitudinal patterns and to get a step closer to providing a strong test of the niche conservatism hypothesis.

Missing from essentially all of the above work is an actual mechanistic or physiological demonstration that cold temperatures matter. Pither (2003) perhaps was the closest to this, as he compiled data on freezing tolerance for temperate trees as it related to their distributions. Similarly, recent work by Zanne et al. (2014) attempted to address this issue by reconstructing the timing of trait evolution on a large phylogenetic tree of plants for traits related to freezing tolerance. This information was then related to spatial distributions for the species ultimately to highlight the key steps the angiosperms needed to take in order to invade freezing environments. However, several issues with how the data were cleaned and analyzed and how they were interpreted were highlighted by Edwards et al. (2015). Thus, there are still uncertainties

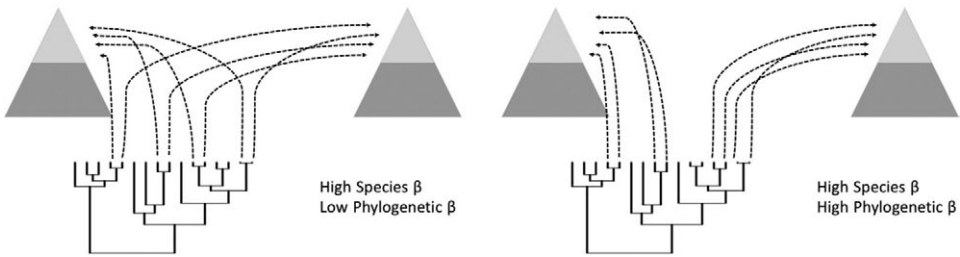


FIGURE 6.2. An example of two possible evolutionary scenarios underlying the composition of assemblages on two different mountain peaks. On the left, there is high species beta diversity and low phylogenetic beta diversity, such that dispersal and niche conservatism are likely important for generating community structure. On the right, there is high species and phylogenetic beta diversity, indicating that colonization and subsequent diversification underlies community assembly.

with how much confidence we can place in the inferences from Zanne et al. (2014), but it still stands as useful contextual information that can be used for future investigations into the latitudinal gradient as it relates to freezing and niche conservatism.

The real question for the niche conservatism–latitudinal diversity gradient research program is: Where do we go from here? We now have a pile of papers showing gradients in clade age, but that is not enough to clearly support the hypothesis. Furthermore, it is unclear exactly how a continuous gradient in clade age conceptually aligns with a discrete abiotic barrier (i.e., freezing). That is, why is there a gradient in clade age from Costa Rica to Mexico? Or why is there a gradient from Tennessee to Ontario? Thus, some more conceptual development or additional analyses are needed to make it clear why the pattern reported is actually a good indicator of the mechanism or mechanisms discussed. Detailed physiological investigations would be useful, but they would be logistically difficult to accomplish. None of this is to say that I don't think niche conservatism plays a major role in explaining the latitudinal gradient in species and clade diversity, but the current state of the concept and data patterns are not enough to feel confident that we have solved the issue. It is hard to determine how all of this can be resolved, but perhaps macroecology would be best served by coming up with alternative hypotheses, alternative tests, and a refining of concepts.

6.2. Phylogenies and the Cradles versus Museums Hypotheses

Closely related to the question of whether phylogenetic niche conservatism explains the latitudinal gradient in species diversity is the question of whether the tropics act as a cradle or a museum of diversity. The central question is whether high origination (i.e., speciation) rates in the tropics relative to the temperate zone explain the latitudinal gradient (i.e., the cradle hypothesis) or whether relatively lower extinction rates in the more stable and climatically benign tropics explain the gradient (i.e., the museum hypothesis). As we can see, the question seeks to determine which component of net diversification rates (speciation versus extinction) is of greater importance in the tropics versus the temperate zone. We can also see, though, that this effectively treats time as equivalent, such that the time for net diversification has been equivalent between the regions. This assumption is flawed, as it has been documented that tropical regions have covered a great extent of the globe for long periods of time. Fine and colleagues have considered this information in the context of the global distribution of plant diversity, and have come to the conclusion that time integrated with available area were better indicators of

species richness among floristic zone as compared to other predictors (e.g., productivity) (Fine and Ree 2006; Jetz and Fine 2012).

The "cradles versus museums" terminology is credited to Stebbins (1974), as is the question in many cases. However, as pointed out by Stenseth (1984), the mechanism and question was subject to discussion via Matthew (1915) and Darlington (1957) prior to Stebbins (1974). When it comes to patterns in data, the connections between niche conservatism and cradles-versus-museums become clear. Specifically, if all else (e.g., species rate) is equal, then lower tropical extinction rates should lead to older lineages in the tropics. This pattern would then be consistent with the patterns of clade age usually reported as evidence for niche conservatism. However, this conflates the two when they are not necessarily the same. For example, the mechanism of lower extinction rates does not directly link to the difficulty in evolving freezing tolerance. Certainly, glacial cycles likely increased extinction rates in the temperate zone, but again, this typically isn't the mechanism directly linked to niche conservatism. The alternative hypothesis is that speciation rates are accelerated in the tropics when all else (e.g., extinction rates) is equal. This would lead to, on average, younger clades in the tropics, which would be misaligned with the patterns expected from niche conservatism. The point here is that while the patterns of clade ages may seem to be related to strong tests of the two mechanisms, they are not actually tests of these hypotheses.

How, then, do researchers test the museum versus cradle hypotheses with phylogenetic information? Ideally, tests of the hypothesis would be able to disentangle the components of net diversification rates (i.e., speciation and extinction rates) in a clade or clades across latitude. In some instances, this type of investigation has been eschewed when a large and rapid radiation has been reported; for example, the dramatic radiation of the Neotropical tree lineage *Inga* (Fabaceae), where ~300 species have been derived over roughly the past 10 million years (Richardson et al. 2001). In this instance, it would appear clear that spectacularly elevated speciation rates occurred in the tropics. However, let us contrast this with another hyper-diverse tropical woody plant lineage, *Psychotria* (Rubiaceae). This genus is relatively old, ~30–40 million years old, but contains over 1,500 species worldwide. From this information alone, we could perhaps say that net diversification has been incredibly high, as there are few angiosperm genus that reach this level of diversity. However, we have little to no information about the timing and magnitude of speciation and extinction rates through time. This brings us back to estimating speciation and extinction rates. This could be estimated reasonably from the fossil record if it were far more complete, but this is not the case for most groups. Thus, we must turn to phylogenetic information.

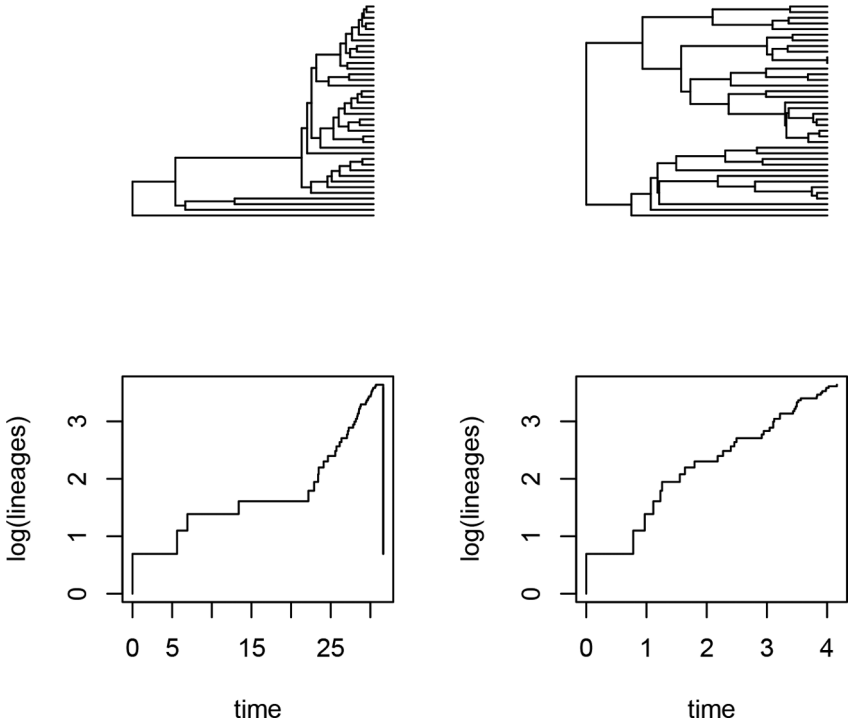


FIGURE 6.3. Two hypothetical lineage through time plots. On the left, there is a rapid accumulation of lineages relatively recently, indicated by the accelerating in the curve. On the right, the curve consistently accumulates, indicating consistent net diversification rates.

Lineage through time (LTT) plots have been used extensively in the past to quantify speciation and extinction rates (Harvey et al. 1994; Nee, May, and Harvey 1994; Nee, Holmes, et al. 1994). Under this approach, the number of lineages (i.e., branches) is recorded on the *y*-axis for a series of time slices (*x*-axis) starting from the root node and moving toward the tips (fig. 6.3). Thus, the line on the graph will increase as lineages accumulate through time from one to the number of tips. Generally, the *y*-axis is log-transformed for visualization and analyses. If the extinction rate is assumed to be zero, which is unrealistic, then the slope of the line connecting the first and last data point in the graph equals the speciation rate. However, an extinction rate of zero is unlikely in most cases, and if a roughly straight line occurs on this semi-log plot, then a model with a constant speciation and extinction rate may be reasonable. Note that a constant net diversification rate does not have to indicate constant speciation and extinction rates. If a constant rate model seems reasonable, then constant speciation and extinction rates may be estimated

from the joint probability surface of lineage birth rate minus death rate and the ratio of lineage death rates and birth rates. From these joint estimates, the individual speciation (i.e., birth) and extinction (death) rates can be calculated. Thus, one may potentially use such an approach to compare speciation and extinction rates between lineages, with some occupying tropical and some occupying temperate zone latitudes. Similarly, one could test for shifts in rates as lineages have colonized new adaptive zones (e.g., Simpson 1944; Ricklefs 2006; fig. 6.4). However, there are limitations to this approach. For example, speciation and extinction rates are typically not constant in the fossil record, which will lead to faulty or imprecise estimates.

Recent methodological advances have been made to allow for the detection of changes in diversification, speciation, and extinction rates through time. For example, Rabosky (2006) introduced a maximum likelihood framework for this purpose. More recent work by Rabosky has applied Bayesian model evaluation to this problem with the inclusion of trait information, thereby potentially helping a researcher link trait evolution to changes in speciation and extinction rates (Rabosky et al. 2014). There is some controversy regarding this method in the literature (Moore et al. 2016), however. I will not cover that controversy here, but a user would do well to read both the original critiques and the responses by Rabosky prior to using the approach. Finally, I would also state that there is some uncertainty regarding how well

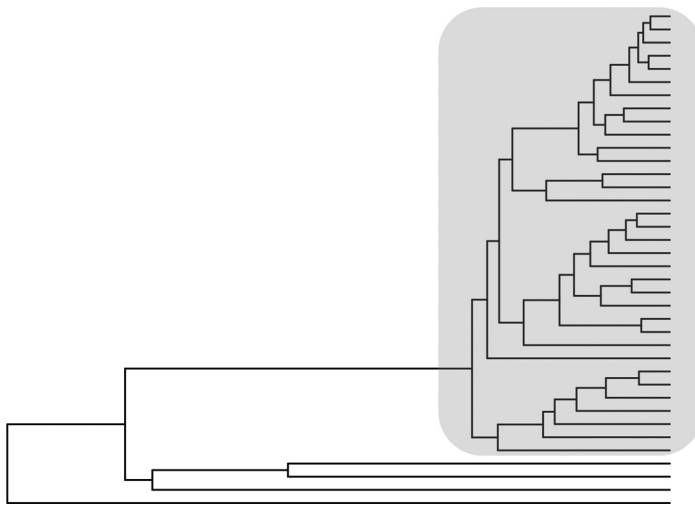


FIGURE 6.4. A hypothetical example of a clade radiating once it enters a new adaptive zone. Specifically, a lineage may colonize a new habitat or region where there is substantial ecological opportunity, thereby accelerating net diversification rates relative to the sister lineage that did not colonize the new zone.

rates of extinction can truly be estimated using such methods including some uncertainty outlined by Rabosky himself (Rabosky 2010).

While we undoubtedly will continue to advance and argue about methods for estimating speciation and extinction rates from phylogenies, we should also consider whether we must continue to debate museums versus cradles. Specifically, like most dichotomies posed in the ecological and evolutionary literature (e.g., niche versus neutral), the answer is that both occur. Indeed, Stebbins (1974) indicated that the answer was not one or the other, and recent work and opinions have reinforced this viewpoint. There simply will be lineages that behave differently, and all of them contribute to the extraordinary tropical diversity. Perhaps more interesting questions are what sets the stage or promotes extraordinary bursts in diversification, and whether there is a limit to the number of species produced from a clade. For example, how did genera like *Inga* or *Costus* (Costaceae; Kay et al. 2005) diversify so quickly? Was this due to specialized interactions with pollinators or pests or due to range fragmentation due to recent climatic oscillations? Additionally, does it seem reasonable to assume that a clade or even a region has a carrying capacity with respect to species richness? These are perhaps more interesting questions where phylogenetic information must play a central role, and the upstart might be better served focusing on these more detailed and conceptually interesting questions.

6.3. Priority Effects, Niche Preemption, and Ecological Opportunity

In the previous sections, I have discussed gradients in diversity along major gradients and how phylogenetic information is relevant to major hypotheses regarding niche conservatism and rates of net diversification. As we have seen, support for these hypotheses often varies between lineages or clades, indicating that additional information is relevant. Here, I will discuss how the timing of colonization might influence the dominance of lineages in present-day ecosystems.

Priority effects are generally considered in the context of community dynamics on shorter time scales (Fukami et al. 2015). They describe situations where the relative order of arrival impacts ecological outcomes. For example, if two roughly equivalent species arrive in an area at different times, the first-arriving species will build up its population size, occupy more physical space, and by the time the second species arrives, it has little resources or space to increase its population size. In this manner, priority effects could impact the relative abundance distribution.

In an island biogeography context, the arrival of one species early may

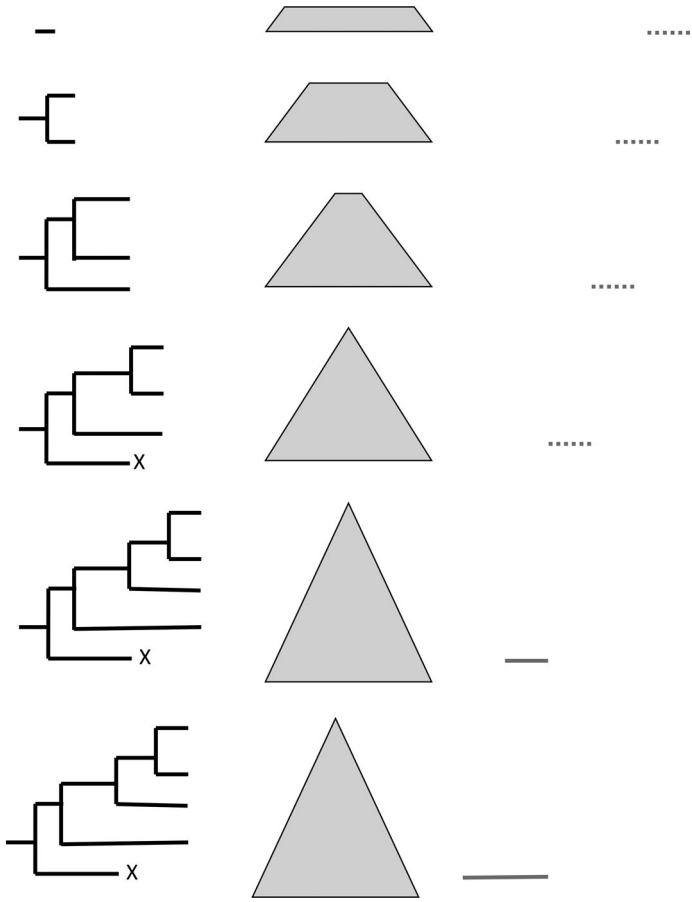


FIGURE 6.5. A hypothetical example where lineages are attempting to colonize habitat on an island. The island is the gray polygon and grows in elevation as it emerges from the ocean. The black lineage on the left colonizes low-lying habitats early on and diversifies into higher elevations through time (depicted from the top of the figure to the bottom). The lineage on the right (dashed line) repeatedly attempts to colonize the island's low elevations, but is prevented from doing so due to the presence of the other lineage. At the fourth time slice, the low-elevation lineage on the left goes extinct, leaving open the opportunity for the right lineage to colonize.

preclude the arrival of another similar species via niche preemption. In this scenario, there is no adaptive evolution of the first species needed to preclude the arrival of the second similar species (fig. 6.5). However, this model can be extended to include a situation where a single colonization leads to an adaptive radiation due to ecological opportunity where the newly evolved species now preclude the arrival of colonists that were dissimilar to the original colonist, but that now are similar to the new species. Similarly, the adaptive radiation may not prevent the colonization of another lineage, but it may

suppress it from rising to dominance with respect to space, abundance, or species richness. Thus, the concept of priority effects due to niche preemption can permeate ecology from community dynamics to adaptive radiations and differential ecological dominance. Critical to this work is a phylogenetic framework that can be used to infer the dispersal events and their timing as well as information regarding diversification rates. While there have been few studies linking priority, radiation, and dominance together, in the following I will provide examples from the literature that directly or indirectly speak to these linkages and discuss pathways for future research.

The first examples I will discuss come from Silvertown and colleagues examining phylogenetic patterns in the endemic floras of Macaronesia and the Canary Islands (Silvertown 2004; Silvertown et al. 2005). In short, they highlight evidence in these floras that most large radiations are monophyletic. The most reasonable inference from this pattern is that a single colonization event occurred prior to the radiation. The authors then go on to argue that in these particular systems, unlike systems like the Hawaiian Islands, barriers to dispersal are low. From this, they argue that there must have been multiple secondary colonization attempts from these lineages that have failed, and that this is likely due to priority effects and niche preemption. This work and the inferences made have been called into question by multiple authors (Carine et al. 2004; Herben et al. 2005; Saunders and Gibson 2005), with the critiques questioning the sampling and the likelihood that preemption could happen. These critiques also suggest that secondary colonization events may have contributed to the radiation via hybridization. These are all reasonable concerns. First, monophyly could be overturned if taxonomic sampling is not complete. Silvertown et al. (2005) claim that the sampling is adequate and often complete, such that this is likely a minor issue. The second critique, I find the most compelling. Specifically, is it reasonable to expect that competition is so precise and strong that a secondary colonist could never be established? The likelihood of this occurring would increase with time between colonization events, and if closely related (i.e., congeneric) species are compared. This is somewhat the case in the work critiqued, which may make it less compelling. However, in other systems, this critique would be much more difficult to refute. In other words, is it really competitive exclusion or simply a failure to arrive at the island in the first place? Third, hybridization has been shown to be an important factor in adaptive radiations (e.g., Seehausen 2004; Mallet 2009; Stankowski and Steisfeld 2015) and certainly should be considered, but it isn't clear, to me at least, why this is in opposition to preemption. Rather, preemption is simply carried out by residents competing for pollination by the new colonists, and leads to the failure of a pure population to persist. In

sum, while the work by Silvertown and colleagues (Silvertown 2004; Silvertown et al. 2005) on preemption of island floras has some mostly unavoidable flaws and uncertainties, it remains an interesting and useful demonstration of the potential importance of priority and preemption.

A second series of important works on priority and preemption that I will discuss comes from the flora of New Zealand. Inspired by the work of Silvertown (2004), Lee and colleagues embarked on a research program not focusing on monophyly per se, but rather on the timing of lineage arrival on New Zealand and how this may be linked to ecological dominance. The first paper assembled generic and stem ages, not crown ages, to infer the timing of colonization and not the beginning of the radiation. This information was then correlated with the species richness and relative abundance (measured as percent cover) of the species from these clades in New Zealand alpine communities (Lee et al. 2012). Their work showed that older lineages (i.e., earlier arrivals) had higher relative abundance, but no difference in species richness. Thus, there was mixed support for the priority and preemption hypothesis. Important deviations of this work from that of Silvertown (2004) include the focus on preemption of a genus by another genus rather than preemption between congeners and the focus on the timing of arrival. The extension to generic competition is interesting and assumes that radiations are extensive enough as to occupy niche space previously only occupied by other genera in other regions. The use of node ages introduces several challenges given the uncertainty in the age estimates, but in subsequent work the research team has confronted this issue more convincingly (e.g., Tanentzap et al. 2015). The lack of a clade age and species richness relationship is not that surprising. A unimodal relationship is often reported, which would conceptually align with the origin, expansion, and demise life cycle most lineages must go through (Levin 2000). Other work claims there is a clade level carrying capacity or density dependence (e.g., Rabosky 2013; Pyron and Burbrink 2013), but such equilibria are unlikely to hold over substantial periods of time. In other words, such work is only capturing the first half of a lineage life cycle.

Priority effects with respect to adaptive radiations in the New Zealand flora have subsequently been examined across different life forms and in the context of the environment. Specifically, Leopold et al. (2015) argue that priority effects should be less important in stressful environments, and buoy this argument by showing less dominance via abundance by older clades in higher elevations and precipitation levels. Later work by Brandt et al. (2016) showed that this relationship was consistent in angiosperms and the reverse in pteridophytes, which likely reflects the fundamental physiological and life

cycle differences between these groups that impact what environments may be considered more "stressful."

A final piece of the New Zealand priority effects puzzle that has been analyzed is the niche space or ecological opportunity experienced by lineages as they arrived. Tanentzap et al. (2015) attempted to address this issue in a couple of different ways. One was to reconstruct the environments of New Zealand through time using oxygen isotope data from planktonic deposits and by using reasonable estimates of the range of elevations in New Zealand over the past 20 million years. A complementary approach was to estimate the niche space occupied by genera over time using known present-day locations, present-day environmental data at those locations, and paleoreconstructions of niche space. From this evidence, the authors conclude that older genera have occupied more niche space, and this broad occupation slowed the diversification and march toward ecological dominance attempted by later-arriving lineages.

The examples of priority effects I have discussed thus far come from insular systems. The use of insular systems has been a theme throughout this book, but so too is the warning that while these systems are tractable, they may not always be representative of mainland systems. Priority effects on the mainland can be difficult to demonstrate, as dispersal histories are complex and phylogenetic information is often not of high enough quality to make definitive statements. However, the closure of the Panamanian Isthmus and the Great American Biotic Interchange (GABI) is one natural experiment allowing for insights (Stehli and Webb 2013). The most obvious case in this context is the asymmetrical distributions of marsupial and placental mammals between North and South America. Specifically, placental mammals were able to invade the south more successfully than marsupials invaded the north. This asymmetry may indicate that the strength of priority due to competitive effects is itself asymmetric. Such effects have been shown in sister pairs of bird species expanding their ranges post-glaciation in North America and meeting in the Great Plains, where eastern species are abiotically limited from expanding westward and western species are competitively excluded from the east (Swenson 2006). Thus, one reasonable interpretation of the mammalian distributions is that placental mammals competitively preempted marsupials, but not vice versa. The lack of reciprocal exclusion, however, may indicate that competitive preemption is not the main causal agent. Rather, predation may have been a key driver of the asymmetry, with the most successful marsupial invasions of the north being large and/or arboreal species. Similarly, asymmetrical spread of disease and susceptibilities may have produced the pattern. Finally, speciation of successful northern lineages in the south

is another non–mutually exclusive possibility. Thus, while preemption or priority may well have been important during the GABI, it was asymmetrical and not necessarily linked to niche preemption or competition.

The GABI can also be utilized to understand priority with respect to plants. Here, spatial distributions may appear to be enlightening. Several genera and families are highly diverse in South America, but far less diverse in Central America and the Caribbean. Furthermore, in those instances where phylogenetic data are available, the South American members of the clade may be monophyletic. Thus, we may look at families like Lecythidaceae that are very diverse in the Amazon and hardly exist in Central America, or genera like *Protium* (Burseraceae) that may indicate failures to dominate northern latitudes due to priority. However, without detailed phylogenetic information, these inferences are weak. For a good example of this, we turn to the genus *Guatteria* (Annonaceae). This large genus is common in South America and rare in other regions and apparently monophyletic in South America. Thus, we might consider this a good example of a lineage that failed to dominate northern assemblages due to priority effects. However, when a robust phylogeny for the group was inferred, we see that it likely originated in Central America, subsequently colonized South America, and greatly radiated (Erkens et al. 2007). Thus, while several patterns may point to priority, detailed phylogenetic information may overturn the inference and open up new questions. For example, the key question here is what it was about the Amazon basin that promoted such a rapid radiation. The point of this example is not to say that priority was not important for plant lineages radiating in Central America versus South America. Rather, I use this example to point to the importance of detailed phylogenetic information and not simply looking at the distribution of species richness in a clade and monophyly.

The possibility of priority effects due to adaptive radiations having long-term impacts on regional assemblage compositional structure, dominance, and congeneric richness is intriguing. There is evidence supporting this mechanism primarily from insular systems, but there are also several research obstacles that limit the strength of the inferences—some that can be overcome and some that cannot. The generation of detailed phylogenetic, fossil, and spatial data can overcome some of the obstacles where patterns of species richness alone may mislead us. However, demonstrating that a lineage truly preempted another is largely impossible, as this represents an interaction occurring millions of years ago where the competitive abilities, niche preferences, and available habitats cannot be known in satisfactory detail. Similarly, the timing of events (i.e., dispersal and diversification) will always be uncertain, due to uncertainty in dating phylogenies and incomplete

fossil records. Thus, the study of biogeographic or evolutionary priority will remain an intriguing possibility and worthy of study, some inferential limitations likely cannot be removed, and phylogenetic information, while helpful, alone cannot provide firm conclusions.

6.4. Conclusions

In this chapter, I have ventured to outline areas where phylogenetic information proves useful for those ecologists seeking to uncover the drivers of gradients in species richness and ecological dominance. The hypotheses and mechanisms discussed include phylogenetic niche conservatism, time, and priority. In each of these cases, the inclusion of phylogenetic information greatly refines the inferences that can be made. However, I hope I have also made clear where, even with this information, the inferences are potentially flawed. Such is the nature of historical analyses in ecology, but this should not deter us from pursuing the hypotheses and questions addressed in this chapter. Much like the discussion of community assembly and the phylogeny as a backbone approach, the benefits of integrating historical and evolutionary information into ecological studies far outweigh the costs imposed by the limitations I have outlined. Synthesis will arise through this continued integration, and stating clearly the limitations will ensure that progress is not slowed.

7

Functional Phylogenomics for Ecology

All too frequently over the past decade I have had colleagues working in evolutionary and molecular biology tell me that next-generation sequencing will change everything. That the cost of sequencing will fall so dramatically that even lowly ecologists will be able to make use of the latest and greatest genomic tools. I must admit that in almost all of those conversations, I ignored what I was being told. It wasn't until about seven years ago that I became intrigued by these conversations. It took some serendipity, some willingness of genomicists and bioinformaticians to informally and slowly introduce me to what is possible, and some willingness of a very few to share with me how much data and funding I might need to accomplish the types of 'omics research (on non–model organisms) I thought might actually be of interest to ecologists. I quickly found that with enough money, a great amount of data could be generated, but in most cases those telling me what types and amounts of data could be generated didn't have a great grasp of ecological concepts or questions. In sum, my ramp-up to being interested in 'omics in ecology has been gradual and skeptical. However, I have now become rather enthusiastic about the integration of 'omics and ecology in non–model species (Swenson 2012b; Swenson and Jones 2017), and in this chapter I will discuss an approach that I think could be very useful for the future of phylogenetic ecology–functional phylogenomics.

Functional phylogenomics can be defined as the use of functional genomic (i.e., transcriptomic) information for phylogenetic inference. As I will describe below, in many cases, the inference of a species tree is the primary goal of a functional phylogenomic investigation. However, the approach has a great range of possibilities that are potentially of great relevance to ecolo-

gists. Specifically, transcriptomic information provides a rapid and broad assay of function in a given tissue (Wang et al. 2009), which can then be compared across species in a phylogenetic context (Lee et al. 2011). In other words, comparative functional analyses are possible, analyses of functional evolution are immediately possible, and broad assays of function that can greatly complement existing functional trait approaches are possible. Thus, I think functional phylogenomics has the potential to greatly mitigate or even completely overcome some of the issues that plague phylogenetic ecology as well as functional trait ecology (Swenson 2012b, 2013). Functional phylogenomics is still a fairly young field, and my enthusiasm may well prove misguided, but I feel a discussion of how this approach has already been integrated into ecology and can be the future of ecological research is in order.

7.1. A Brief Recap of Research Challenges for Phylogenies in Community Ecology

In this volume, I have identified two approaches for utilizing phylogenies in community ecology. The first approach, which I have termed the phylogeny as a proxy approach, has been utilized for roughly a century in community ecology and biogeography. Under this approach, relatedness is used as a proxy for ecological similarity and similarity is used to infer the relative importance of abiotic and biotic interactions for community assembly. For example, if closely related species co-occur, this may indicate that they are ecologically similar and, therefore, competitive superiority or abiotic filtering may explain their co-occurrence. Conversely, if distantly related species co-occur, this may indicate that they are ecologically dissimilar and co-occurrence is promoted by assembling species that maximize their niche differences. This approach suffers from many problems. Principal among these is that phylogeny may not always reflect similarity. Evolutionary convergence is frequently reported in the literature, and there are classic examples of such convergence where relatedness measures alone would lead one to infer the polar-opposite mechanism. A pragmatic view might be that phylogenetic relatedness represents the average phenotypic similarity, which is a valid assumption particularly on meso- or large taxonomic scales (e.g., Cavender-Bares et al. 2009; Swenson 2011a; fig. 7.1). However, the overall average phenotypic similarity likely does not dictate co-occurrence. Rather, one to a few traits or niche axes are likely the key, and these traits or axes are also likely those to diverge to the greatest degree around the time of speciation (Sobel et al. 2010). Thus, an average measure of similarity is not enough analytically or conceptually to solve the puzzle of species co-occurrence patterns.

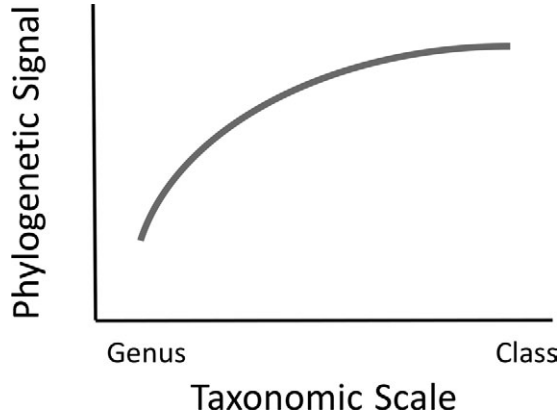


FIGURE 7.1. The general relationship between phylogenetic signal and taxonomic scale, as inspired by Cavender-Bares et al. (2009).

The second approach I have termed the phylogeny as a backbone approach. This approach seeks to map trait or niches onto phylogenies to quantifying their evolutionary history. This information is then aligned with co-occurrence data to ask how this evolutionary history has impacted community assembly. For example, have distantly related species converged in their phenotypes in order to co-occur in a given environment, or has a lineage colonized a location and undergone rapid phenotypic divergence to maximize niche differences and the probability of co-occurrence (e.g., Losos et al. 1998)? Thus, the phylogeny is used as a foundational piece of information essential for evolutionary inferences that can be applied to a community ecology context, but it does not serve as a proxy. This phylogenetic approach to community ecology is far less common in the ecological literature than the phylogeny as a proxy approach at present. I have argued that the phylogeny as a backbone approach should more commonly be applied, and that the use of a phylogeny as a proxy for similarity should not be applied beyond attempting to gain quick and crude insights into the possible similarity between species that must later be validated prior to drawing robust conclusions. However, I have noted that the phylogeny as a backbone approach also has conceptual and analytical challenges that limit progress. One of these challenges is quantifying those aspects of organismal function that are ecologically important. That is, the handful of traits that a functional ecologist typically measures on a particular group of organisms may give a general overview of the ecological strategies of the species sampled, but they are likely a woefully incomplete or sparse assay of organismal function. Thus, the challenge is to conduct broader assays of organismal function on many species.

In sum, there are problems that are unique to the phylogenies as proxies and as backbone approaches, and these problems may be avoided using one approach over another. In large part, the situation is worse for the proxy approach, and using a backbone approach allows one to overcome most problems. However, there is a set of problems that are shared between the two approaches that are not easy to overcome using either approach. Specifically, both approaches frequently rely on very limited assays of organismal function. This may be due to logistical constraints, as it is difficult to measure detailed physiology in the field for tens to hundreds or thousands of species, and laboratory measurements would be nearly as challenging. Thus, there are many aspects of organismal function that we know are important, but we cannot measure them easily, and therefore we do not know their impact on the pattern of interest (Swenson 2012b, 2013). Limited functional assays may also be due to confidence that we, as experts, know the "right traits" to measure, and we therefore only measure those traits. I would propose that such confidence is unwarranted, and that there is a great deal of important functional diversity that we are unaware of (what I would call functional dark matter) and therefore never measure (Yang et al. 2018).

Overcoming the challenge of obtaining broader assays of function across many species quickly has proven difficult. However, ecologists now find themselves at a time and place where technological and computational barriers are eroding rapidly, and this will permit the widespread integration of functional genomics into ecology. Specifically, RNA sequencing (RNA-seq) is becoming cheap and easy enough to perform, and the bioinformatics tools and computational power necessary to analyze RNAseq data from non–model organisms (i.e., the organisms almost all ecologists study and are interested in) are becoming readily available (Wang et al. 2009; Haas and Zody 2010; Robertson et al. 2010; Whitehead et al. 2010; Grabherr et al. 2011; Ozsolak and Milos 2011; Swenson 2012b; Haas et al. 2013; Alvarez et al. 2015; Swenson, Iida, et al. 2017). In brief, RNAseq uses next-generation or third-generation sequencing technology to sequence the mRNA in a tissue sample. This information can be utilized to assemble a transcriptome. In other words, it is a rapid assay of the genes being expressed in a given tissue at the time of sampling. For example, a typical tree leaf transcriptome may contain somewhere in the range of 30,000 to 40,000 expressed genes (Neale and Kremer 2011; Neale et al. 2017). While there are limitations to this research approach and the data produced, which I will discuss below, functional genomics holds enormous potential to transform functional ecology, and when the data are used in a phylogenomic context (i.e., functional phylogenomics), they will open a completely new arena of phylogenetic ecology (Lee et al. 2011). In the

next section, I will describe what exactly functional phylogenomics is, and the inputs and outputs from a typical functional phylogenomic study, such that we can understand how an ecologist may integrate this emerging discipline into their work.

7.2. What Is Functional Phylogenomics?

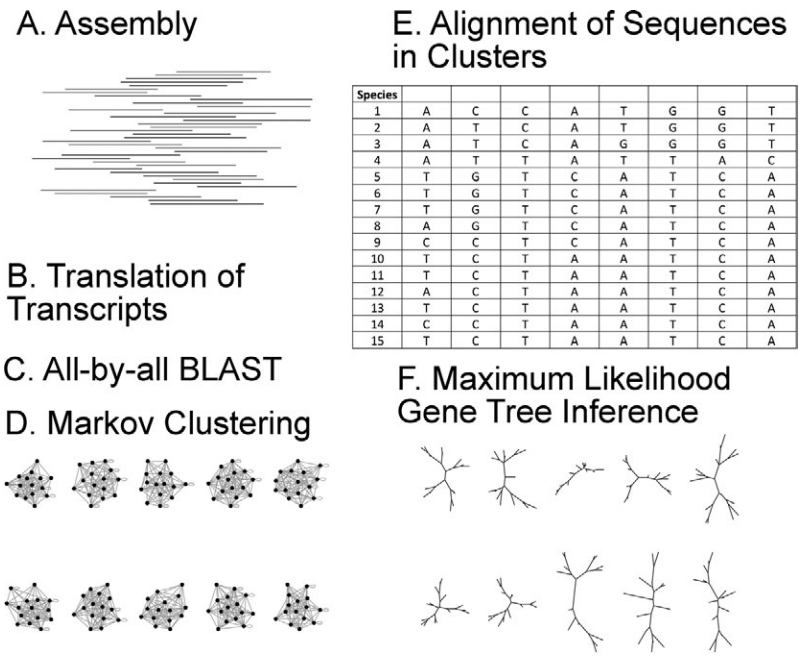
Technological advances that permit the generation of large amounts of sequence data are transforming many aspects of ecology and evolutionary biology. In short order, phylogenetics has transitioned from analyzing one to a handful of DNA regions to building mega-phylogenies pulling from large sequence repositories (e.g., Smith et al. 2009; Beaulieu et al. 2012). Not only has the breadth of sampling increased, but the depth of sampling has also increased. Specifically, phylogenomic studies are becoming more common in the literature, where hundreds to thousands of DNA regions are analyzed to produce gene trees and ultimately to infer a species tree (e.g., Eisen 1998; Eisen and Fraser 2003; Philippe et al. 2005). There are a variety of sequencing approaches utilized in phylogenomics, including genome skimming (Weitemier et al. 2014), anchored phylogenomics (Lemmon et al. 2012), ultraconserved elements (Faircloth et al. 2012), and the use of transcriptome assemblies (Lee et al. 2011).

Functional phylogenomics is the inference of gene and species trees using transcriptome assemblies derived from RNAseq data (Lee et al. 2011). Functional phylogenomics has several aspects that make it potentially more attractive than DNA-based phylogenomic approaches. First, transcriptomes are relatively cheap to sequence and computationally easier to assemble as compared to genomes. Second, no conserved regions must be known a priori, thereby lowering the bioinformatic burden or gatekeeping. Third, the gene trees utilized are generated using functional genes expressed in the species. Thus, the degree of sequence similarity between the species is informative for reconstructing species relationships, but it also can roughly reveal the functional similarity of species for hundreds to tens of thousands of genes.

There are several potential pitfalls lurking in functional phylogenomic studies. These include poor annotation of gene trees due to no closely referenced genomes being available, a high degree of functional convergence potentially leading to flawed species tree inferences, and expression differences between species or samples based upon collecting protocols (e.g., time of day, time of year, levels of abiotic stress, tissue type) that may weaken inferences. That said, these weaknesses are likely heavily outweighed by the positives noted in the previous paragraph, and functional phylogenomic approaches

are likely to become common in the near future (Swenson 2012b; Swenson and Jones 2017).

Here, I will briefly outline a prototypical functional phylogenomic study using a broad brush, as the goal is not to get into the fine details of transcriptome assembly and phylogenetic inference. Rather, the goal is to present a general overview of a typical workflow (Yang and Smith 2013, 2014; Yang et al. 2017; fig. 7.2). Then I will present a few examples of functional phylogenomic studies from the evolutionary literature to demonstrate what types of data and inferences are typically produced. The first step of any such study is the sampling of tissue for RNAseq. For most purposes and certainly for ecologically oriented studies, tissue types, sampling times, and abiotic conditions should be standardized as much as possible. Next, transcriptome assemblies are generated from sequencing reads and bioinformatics software. The quality of assemblies, of course, can vary substantially, due in large part to the depth and quality of the sequencing, but also due to bioinformatics decisions (i.e., software and parameters utilized).



Species								
1	A	C	C	A	T	G	G	T
2	A	T	C	A	T	G	G	T
3	A	T	C	A	G	G	G	T
4	A	T	T	A	T	T	A	C
5	T	G	T	C	A	T	C	A
6	T	G	T	C	A	T	C	A
7	T	G	T	C	A	T	C	A
8	A	G	T	C	A	T	C	A
9	C	C	T	C	A	T	C	A
10	T	C	T	A	A	T	C	A
11	T	C	T	A	A	T	C	A
12	A	C	T	A	A	T	C	A
13	T	C	T	A	A	T	C	A
14	C	C	T	A	A	T	C	A
15	T	C	T	A	A	T	C	A

FIGURE 7.2. A generic workflow for functional phylogenomic gene tree inference. The workflow begins with RNAseq and then transcriptome assembly. The contigs from the assembly are then translated, and BLAST (C) is used to compare the sequence similarity of contigs across species. Markov clustering (D) is then used to identify groups of contigs (homologs) that will be aligned (E) and ultimately used for phylogenetic inference.

The contigs from the assembled transcriptomes are then translated into putative peptides. The translated contigs of one sample (i.e., species) are then compared to those from all other species in the study using BLAST (Altschul et al. 1997). The goal of this sequencing matching is to identify homologous sequences between samples (species). The degree of similarity between contigs across species is then clustered to identify homologous sequence groups, which can include multiple contigs per species and may not include contigs from all species. Generally, a minimum number of species is set during this stage, such that homolog groups with too few species represented are discarded. The sequences from each homolog group are then aligned, and a gene tree can be inferred. The inferred homolog gene trees may contain paralogs and gene duplication, and gene family expansion can be quantified. Ortholog gene trees can be produced using different approaches. At this point, a species tree can be inferred using the distribution of gene trees, which may number from the hundreds to thousands depending on the taxonomic sampling and minimum number of species allowed in gene trees.

It is important to note that the contigs themselves are typically compared to annotation databases typically derived from model species and/or reference genomes using an algorithm such as BLAST. In some instances where the focal group is closely related to a model species or well-annotated reference genome, the annotations obtained may be quite reliable. In many instances, however, the species in the study are distantly related to the species in the annotation database. The annotations assigned in these instances are a starting point, but likely to be less reliable (Pavlidis et al. 2012). Annotations may only be assigned to half or less of the contigs in a given species, and the annotations may vary within homolog groups. This adds further uncertainty when interpreting what the patterns from a given gene tree mean, but they do serve as a starting point and may be useful for indicating what unknown aspects of function (i.e., functional dark matter) are of great importance, as I will discuss below.

In the remainder of this section, I would like to highlight some examples of functional phylogenomics from the evolutionary and systematics literatures. These literatures are increasing in size rapidly. I have only selected a couple of examples, as they help elucidate how functional phylogenomic techniques may be useful to ecologists. I apologize in advance to those many researchers whose work I do not discuss. My first introduction to functional phylogenomics came when a colleague of mine, Andy Jones, passed along a reprint of work by Lee et al. (2011) that had just been published in *PLoS Genetics*. Earlier that year, Andy and I had been discussing how to integrate

next-generation sequencing data into forest dynamics plot research, and he passed along this article as something that might spark my interest. Admittedly, it took me a couple of reads before I understood enough of the approach, but it ultimately became clear to me that functional phylogenomics could be integrated with community ecology—in concept. Whether it could be incorporated in practice was unknown to me for years to come.

In brief, the work by Lee et al. (2011) compiled genomic information from 150 plant species from 101 genera. Orthologs were identified by the research team using the pipeline OrthologID, and they generated a matrix partitioned by orthologous genes. A phylogenetic tree for the 101 genera was produced, and support for each node from each gene partition was calculated. The first goal was to reconstruct a phylogeny of the seed plants. The main output from this was the placement of the order Gnetales sister to the gymnosperms. Thus, as with almost all contemporary studies, this functional phylogenomic study had a major goal of reconstructing evolutionary relationships. Next, by assigning ortholog partitions to gene ontologies, the researchers were able to quantify how many partitions per ontology supported a given node. From this, Lee et al. (2011) identified ontologies that had an overabundance of partitions supporting a given node. An overabundance of an ontology from a supported node was inferred to indicate that the given function was important during the diversification of the subtended taxa. In other words, there has been significant diversification of the lineage and the genes in a given ontology. While the identification of the actual gene ontologies was interesting and important, the general concept of mapping the concordance or discordance of functional genes and gene ontologies onto a phylogeny was what intrigued me the most. I will describe why and how this links to ecology in the next section.

In the years since the Lee et al. (2011) article, phylogenomic inference upon the basis of transcriptomic information and the mapping of functional gene agreement with species trees has become more refined and more accessible. An example of work from Stephen Smith, Ya Yang, and colleagues (Smith et al. 2015) principally concerning the plant order Caryophyllales provides a nice example of these advances. As phylogeneticists and systematists, a main goal in their work has been to reconstruct the evolutionary relationships between lineages in the Caryophyllales. To accomplish this, they assembled a data set of hundreds of species with transcriptome assemblies. The work used these assemblies to identify homologous gene groups, to infer homolog gene trees, to infer ortholog gene trees, and to infer species trees. In doing so, they have also generated publicly available code that can be utilized for functional phylogenomic analyses. Further, they have developed and made available

code that characterizes gene tree conflict and concordance with species trees. In other words, a species tree is ultimately inferred, but for each node, gene tree concordance can be quantified. Thus, in a sense, the work is similar to that of Lee et al. (2011), but it does not rely on gene ontology annotations and directly measures the concordance and conflict of individual gene trees and not groups of genes in a given ontology. This greatly refines our ability to understand levels of support within and across ontologies, and to consider the large number of gene trees that have no annotation or annotations from different ontologies. A key finding in their work and that of others is that it is common for many homolog gene trees to conflict with the species tree. While these conflicts and concordances are useful for refining our understanding of the evolutionary relationships between species and the development of more robust phylogenetic inferences (Smith et al. 2015), they are also of potential interest to those studying functional diversity within and among lineages and how this relates to species distributions and co-occurrence. In the next section, I will expand on this as well as describe other ways in which functional phylogenomics may intersect with ecology.

7.3. The Intersection of Functional Phylogenomics and Ecology

As I have described above, the field of functional phylogenomics is largely one that seeks to reconstruct the evolutionary relationships of lineages; in most cases, it seeks to identify the functional gene trees or gene ontologies that support nodes in the species trees, and in some cases, it seeks to develop hypotheses for why a given gene or gene ontology lends support or is overrepresented in a clade. From a macroevolutionary perspective, I find this all very exciting, as more robust phylogenetic inferences are often made and the evolutionary history of organismal function is also described. This second aspect, though, makes this literature far more interesting to me than the traditional tree inference literature.

From the perspective of an ecologist integrating phylogenetic and functional information into their research, there appear to be several synergies between functional phylogenomics and ecology and potential exciting new avenues for research that may help solve some of the problems that vex both the phylogeny as a proxy and phylogeny as a backbone approaches. As mentioned above, the clearest advance and contribution that transcriptomic information would provide ecology is the production of broad and detailed assays of organismal function. These assays would go far beyond that provided by most standard functional trait investigations. As I will discuss in the next section, ecologists using transcriptomics are now able to quickly assay details

of organismal function that are of great interest, but rarely measured adequately. For example, plant ecologists can now quickly assay all of the genes related to photosynthesis and plant defense responses using transcriptomic approaches (e.g., Han et al. 2017; Zambrano et al. 2017). I suspect that such assays will revolutionize functional ecology and quickly transform the literature, where scaling from genes to individuals, communities, and ecosystems will become possible (Swenson 2012b; Swenson and Jones 2017).

A second important aspect of functional phylogenomic approaches for ecologists is that it facilitates comparative transcriptomics. For example, an ecologist may be interested in how their species of interest functionally responds to a new environment or stress. This could be accomplished using measures of anatomical or physiological traits. It may also be accomplished via transcriptomics and measuring differential gene expression in tissue from individuals in the different environments. However, when this hypothetical transcriptomic ecologist seeks to study more than one species, they will quickly encounter a series of problems. The first problem will be attempting to compare the transcriptomic data across the species. For example, species A may have a contig named "trs.813194afd.001" that has strongly increased in expression in the new environment relative to the control, and species B may have a contig named "avw832.0065" that has similarly increased in expression. However, it is unclear what the roles of these genes are in each species, and whether they are the same. One approach to solving this problem is to first assign each contig to gene ontologies and then quantify whether there is a higher than expected proportion of genes in each ontology that are differentially expressed. This analysis is called gene set enrichment, and I have utilized it previously in the context of community ecology (Swenson et al. 2017b). However, such an analysis has clear limitations. First, it relies on gene ontology annotations from distantly related species. These annotations may be unreliable, and a large fraction of genes may not have annotations at all and therefore may not be analyzed. Second, it lumps all genes in an ontology together, thereby not considering how individual genes are behaving. This may be important, as some genes may be significantly higher in their expression while others may be lower in their expression. Standard gene set enrichment tests treat these outcomes as equal because both are significant changes in expression. Third, this approach can allow one to compare species by comparing the outputs of gene set enrichment for gene ontologies across species (Swenson, Iida, et al. 2017), with individual gene ontologies being the cross-species indexing agent, but it does not permit the direct comparison of homologous or orthologous genes across species. A functional phylogenomic approach would solve or, at least, greatly mitigate most of these issues. It

would allow a researcher to conduct their comparative differential expression analyses on the level of homolog or ortholog genes, and it would permit the analysis of all genes irrespective of having annotations or annotation quality. Thus, at present, functional phylogenomics provides the clearest pathway toward powerful comparative analyses of differential gene expression across species while accounting for their shared history (Dunn et al. 2018). As transcriptomics continues to integrate into ecology, comparative gene expression studies are likely to be more common, and a functional phylogenomic foundation will greatly facilitate and improve such research.

A third feature of functional phylogenomics that is of particular relevance to phylogenetic ecology is the tracing of functional gene tree concordance and conflict along species trees. The phylogeny as a proxy approach has several key limitations. The key limitation is that relatedness is used as a proxy for similarity in unknown functions. Proponents of this approach over the phylogeny as a backbone approach may argue that the backbone approaches are limited to studying a few traits thought to be of importance, but they fail to capture important unmeasured aspects of function that may have phylogenetic signal. In other words, while the proxy is not perfect, it holds missing information that may be important. In many respects, functional phylogenomics simultaneously solves both of these problems. First, by tracing functional gene tree concordance discordance, one is able to identify which aspects of function have strong phylogenetic signal and which don't. This information would be very useful for determining when, where, and why a phylogenetic signal derived from a species tree exists in an ecological data set. Second, by analyzing data from whole transcriptome shotgun sequencing, a researcher obtains a broad assay of organismal function, including the functional dark matter that may have phylogenetic signal, which phylogeny as a proxy supporters argue is a benefit of their approach over others. Like any method, of course, there are limitations to the functional phylogenomic approach to community ecology, and it will not resolve all problems. Important limitations will include the depth of sequencing, tissue-specific expression, and the importance of differential expression. If rare transcripts have large ecological impacts, these transcripts may be missed by most ecologists who, for various reasons, may not sequence deeply. Similarly, if genes expressed in a specific tissue (e.g., defense response to fungi expressed only in roots) and the functional phylogenomic analyses are based on samples from another tissue (e.g., leaves), then important ecological interactions may go unnoticed. These two issues may be solved if transcriptome assemblies are generated from multiple individuals and many tissue-specific samples, which will become more common soon as costs fall. They may also be mitigated

by analyzing sequence data from whole exomes rather than transcriptomes. Finally, while there is some evidence that nucleotide similarity scales with expression similarity between species, it may turn out that once more data has accumulated, differential expression and not nucleotide similarity is far more important for understanding how organismal function influences ecological outcomes.

7.4. Existing Examples of Functional Phylogenomics in Community Ecology

The widespread production and analysis of RNAseq data is a recent phenomenon. Thus, functional phylogenomics, itself, is not widespread in the literature. However, I suspect that by the time this book is published, it will be fairly common in the evolutionary and systematics literatures. To my knowledge, as I am writing this, there are exceedingly few examples of transcriptomics being utilized in community ecology that are not meta-transcriptomic studies. The majority of these studies have investigated differential gene expression of species given different abiotic or biotic contexts and how this is linked to species co-occurrence (e.g., Narwani et al. 2017; Swenson, Iida, et al. 2017). I consider these to be some of the most detailed investigations into the functional ecology of species co-occurrence conducted to date. Beyond gene expression studies, I am aware of two functional phylogenomic studies in community ecology—both of which were published in a species feature in the *Journal of Ecology* in 2017 (Han et al. 2017; Zambrano et al. 2017). Here, I will describe each of these studies, as I think they provide good examples of how functional phylogenomic approaches can be used to focus on a particular aspect of organismal function of interest. In section 7.5 of this chapter, I will discuss how less focused studies could be conducted that may be as or more interesting than these two published examples.

The first example is from Zambrano et al. (2017), who studied functional gene sequence similarity across 21 co-occurring species in a forest dynamics plot in a temperate broadleaf forest in the state of Wisconsin. They focused only on gene trees that were annotated as belonging to the defense response gene ontology, and asked whether a focal tree's growth and survival rates were related to the similarity of neighboring heterospecific trees given their "relatedness" on a given functional gene tree related to defense response. The expectation was that the demographic performance of a focal tree would be improved when neighboring heterospecifics were more dissimilar than expected in their functional gene sequences.

The focus on defense-related genes by Zambrano et al. (2017) makes this study of particular interest to tree community ecologists. A major hypothesized mechanism for promoting tree species coexistence is the Janzen–Connell mechanism, where seedling performance is reduced near adult conspecific trees due to shared enemies (Janzen 1970; Connell 1971). Thus, a key, though nonexclusive, pattern consistent with this mechanism should be intraspecific negative density dependence (NDD). Evidence for NDD is widespread in tree communities, to the point that it is no longer surprising or likely to advance ecology much when it is found. Recent work has sought to quantify whether NDD transcends species and whether individual focal performance is negatively impacted when there are neighboring heterospecifics that are similar (e.g., Kunstler et al. 2016; Wu et al. 2016). This similarity should reduce niche differences (i.e., increase interspecific competition) or increase the likelihood of shared enemies.

A difficulty with testing the Janzen–Connell mechanism and associated neighborhood analyses of the importance of heterospecific similarity has been documenting either the shared enemies themselves or the traits of the species related to plant-pest interactions. Rarely has this evidence been adequately collected in even moderately diverse communities. When it has been accomplished, it has required enormous effort. For example, the reconstruction of plant-lepidoptera-parasitoid relationships in tropical forests in Costa Rica and Papua New Guinea has been tremendously successful, but is ongoing after years and years of work. Similarly, inventories of tropical tree-pathogen networks have been conducted painstakingly, but only in a few localities and with substantial effort. In other work, detailed plant defense chemistry has been measured among congeners in a locality to elucidate the importance of plant herbivore networks. This work has been conducted in a few sites and has required detailed clade-specific chemical analyses that would not scale to a diverse community composed of many families quickly. All of this work has been tremendously insightful, and if it could be brought to scale it would be outstanding, but this is unlikely to happen in the near future.

An alternative is to focus on easy-to-measure plant functional traits that may indicate defense investment. However, these are generally very crude measures (e.g., leaf toughness) and may not indicate defense only related to one pest (e.g., herbivores) and not others (e.g., fungal pathogens). Another alternative approach has been to focus on the phylogenetic relatedness of species as a proxy for the degree to which two species share an enemy. Previous work by Gilbert et al. (2012) has shown that there is a higher probability of two plant species sharing enemies when they are less than 50 million years

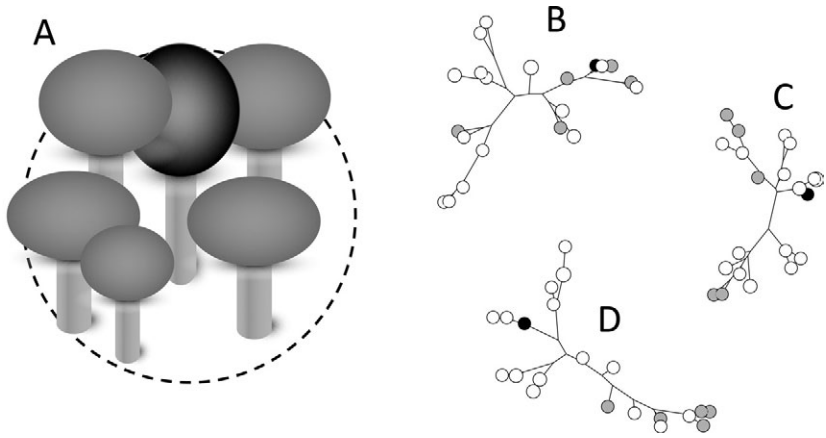


FIGURE 7.3. In this example, a focal tree (black) in A is surrounded by heterospecific trees (gray) in a neighborhood delineated by a dashed line. The performance of the focal tree is related to the functional gene similarity of neighboring hetero-specifics. This similarity can be calculated using branch lengths from functional gene trees generated from a functional phylogenomic approach. For example, for gene trees B and C, the focal species is similar to neighbors, but for gene tree D it is very dissimilar.

diverged. However, as I have discussed throughout this volume, phylogenetic proxies have substantial problems, and phylogenetic signal in one instance does not indicate that phylogenetic signal will be found in every instance.

The work by Zambrano et al. (2017) sought to show how functional phylogenomics could be leveraged to overcome some of the challenges facing those interested in whether neighboring heterospecifics impact focal tree performance upon the basis of their similarity in defense. They used the same standard functional phylogenomic framework outlined earlier in the chapter, but sampled species from a community rather than a given clade. Thus, their study species ranged from gymnosperms to angiosperms. Additionally, they only focused on homolog gene similarity calculated from gene trees containing all 21 species and not similarity from homolog trees not containing all species or from ortholog gene trees (fig. 7.3). From their workflow, they obtained a total of 27 homolog gene trees that had annotations belonging to defense response. Genetic similarity for 16 and 4 of these genes for heterospecific neighbors negatively impacted focal tree growth and survival, respectively. That is, their study was able to identify the genes related to plant defense that were linked to heterospecific NDD, presumably due to shared enemies. The approach by Zambrano et al. (2017) is not without some problems, and further work should be done to validate their approach. For example, the work hinges on the assumption that the defense response annotations, assigned using data from distantly related species, are valid. Further, differential ex-

pression of defense response genes may be more important or overthrow the results derived from examining only sequence similarity. Thus, future studies that quantify expression in natural or experimental settings and validation of the genes by inducing defense responses on the study species would prove valuable. Nonetheless, the work serves as a completely new way to assay and compare those aspects of function that are linked to a major hypothesis, but go unmeasured or poorly measured across entire communities.

The second example of functional phylogenomics being applied to community ecology comes from Han et al. (2017). This work focused on the co-occurrence and demographic rates of seedlings from 101 angiosperm tree species in a subtropical forest in China. The number of species with assembled transcriptomes in this single ecological study alone is impressive, as only a few years earlier a major multi-institutional effort was undertaken to sequence and assemble 1,000 plant genomes called "1KP." In other words, a single group of community ecologists over the course of a year sequenced and assembled 10% of that accomplished by 1KP. This does not reflect the relative expertise or abilities of the two groups. Rather, it reflects rapid changes in sequencing costs and the availability of computational infrastructure and powerful bioinformatics tools. The Han et al. (2017) study utilized the same analytical workflow as that used by Zambrano et al. (2017), with the exception that they focused on gene ontologies related to photosynthesis and quantified the overall number of shared homolog groups between species rather than gene tree relatedness per se. Thus, the selected homolog gene trees were related to photosynthesis and were utilized in neighborhood models like those used in Zambrano et al. (2017).

The research by Han et al. (2017) focused on genes related to photosynthesis for several reasons. First, obviously, light capture is essential for growth and survival in tree seedlings that live in heavily shaded understory environments. Previous work has demonstrated that differential responses to light levels influence tree seedling success and ultimately co-occurrence in forest communities (e.g., Kitajima 1994). Second, the photosynthetic rates and life-history strategies are commonly estimated using one to a few traits from the leaf economics spectrum (Reich et al. 1997). For example, species with high specific leaf area (cm^2/g), nitrogen content, and phosphorus content tend to have faster photosynthetic rates, but shorter leaf life spans. These "acquisitive" species contrast with species with low specific leaf areas and nutrient content but longer leaf life spans. However, the mechanistic linkages between these traits and photosynthetic rates have been questioned (e.g., Osnas et al. 2013), and certainly photosynthesis is a series of reactions not easily captured

by measuring a single leaf trait. An alternative approach to measuring traits like specific leaf area is to conduct sophisticated photosynthetic measurements in the field with a LiCor instrument or similar. Along with the enormous cost of these instruments are the logistical difficulties of making such measurements on hundreds of species in a short period of time.

Using a functional phylogenomic approach, on the other hand, Han et al. (2017) were able to identify genes related to the light and dark reactions and responses to light of varying qualities, among others. In other words, using their approach, one can identify the genes related to photosystems, electron transport, ATPsynthase, and the Calvin Cycle, as opposed to knowing the ratio of leaf area to mass. This represents a substantial leap forward in the depth and breadth of the assay of organismal function in a community facilitated by functional phylogenomic approaches.

A total of 15 gene ontologies were examined by Han et al. (2017). Of these, three were found to be important for neighborhood interactions and focal seedling performance in the forest plot. Specifically, the results showed that when a seedling was surrounded by heterospecific neighbors that shared more than expected homologous gene groupings, they had higher survival rates. This was indicative of a competitive hierarchy where species with genes related to shade tolerance performed better in certain environments than species with dissimilar genes. This conclusion was further bolstered by partitioning species into light- and shade-demanding species and through consideration of canopy openness measurements. Like the work of Zambrano et al. (2017), this work suffers from having to rely heavily on annotations from distantly related species and not capturing the dynamic functional response (i.e., differential gene expression) of the individual plants. Additionally, this study would have been improved if phylogenetic branch lengths rather than number of shared homolog groups were used. However, it also provided an investigation with unprecedented detail into how genes related to an important aspect of plant function influence species co-occurrence and community assembly.

Here, I have presented the first two examples integrating functional phylogenomics and community ecology. While there were only two examples, I think they demonstrate the power of such an integration, and that community functional phylogenomic approaches are feasible for ecologists studying diverse systems full of non–model organisms. As financial and technological barriers continue to erode and more well-annotated reference genomes are published, this approach will only become more powerful and commonplace in the ecology literature. In the next section, I will provide a vision for where I think this literature might go, and the areas most likely to be fruitful.

7.5. Future Directions

In the previous section, I described the only two functional phylogenomic investigations in community ecology at the time I am writing this chapter. Given the pace at which all things 'omics move forward, many others may be published between now and the time this book is in print. This may make some of the future directions to be described in this section quaint or downright boring. Nevertheless, here I will outline what I can imagine are some of the more interesting future possibilities that await those interested in integrating functional phylogenomics into ecology.

The first clear future direction is to make full use of all of the gene trees produced by a functional phylogenomic analysis in community ecology. In the two studies described in the previous section (Han et al. 2017; Zambrano et al. 2017), only certain annotated functions were analyzed. For example, Zambrano et al. (2017) produced over 5,000 functional gene trees in their study, but fewer than 30 were analyzed. One approach for the future would be to focus on a series of functions of interest (disease resistance genes, photosynthetic genes, drought response genes, etc.) instead of just one. Ideally, such a study would be grounded in a priori expectations regarding how these functions should influence community structure and dynamics. Alternatively, one could blindly search through all gene trees to find those that were the best predictors of the ecological outcome of interest. This type of blind search or "fishing expedition" may be antithetical to some, but it is a reasonable approach presently. Such expeditions are nothing new to 'omics researchers that often begin and end with no clear hypotheses driving their work, but the distain for such work in ecology leads me to explain why it might be valid in functional phylogenomics work. A major reason for this is that it is nearly impossible to have a priori expectations about genes that have no known function. Note that when I say "no known function," it does not mean these are not functional genes. Rather, a valid annotation of a gene could not be achieved given information derived from well-studied species such as those with reference genomes and model species. As it turns out, such genes are common in functional phylogenomics of communities. For example, in the Zambrano et al. (2017) study, roughly half of the 5,000 gene trees had no annotation. A great advantage of transcriptomic investigations, in general, and in ecology, specifically, is that they provide broad assays of what parts of the genome are being transcribed irrespective of whether the function is currently known. If these unannotated genes are found to be important predictors of a given ecological pattern or response, then they can be targeted as genes for future study and given a preliminary annotation. There-

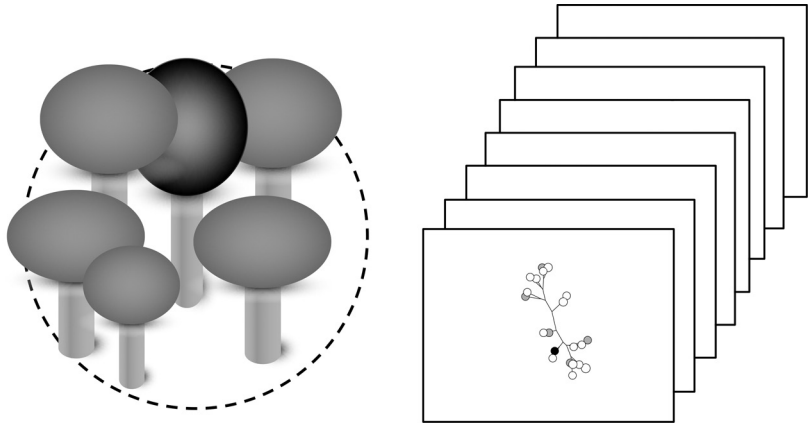


FIGURE 7.4. In this example, a focal tree (black) in A is surrounded by hetero-specific trees (gray) in a neighborhood delineated by a dashed line. The performance of the focal tree is related to the functional gene similarity of neighboring heterospecifics. In this example, the researcher considers thousands of gene trees blindly instead of focusing on just a few gene trees with a known function of interest.

fore, ecological candidate genes can be identified using such an approach. Thus, it would be interesting to conduct a functional phylogenomic study of a community where all gene trees are utilized, annotated, and not annotated, to determine how frequently unannotated genes (i.e., functional dark matter) are actually strong predictors of the ecological outcome of interest (fig. 7.4). Finally, I suspect that fishing expeditions may be useful for ecologists, as they may not be expert enough in cellular physiology to have a clear understanding of how each of the thousands of functional genes in a data set may impact an ecological interaction. Thus, a more efficient approach may simply be to examine all genes simultaneously, identify those that are the most predictive, and then consult the literature and/or a colleague to gain insights into the gene and how it might logically connect to ecology. If this connection is unclear, then the ecologist should report the result, but she or he should simultaneously avoid attempting to concoct a story about why this particular gene is important.

Next, if phylogenetic ecology moves in the direction that I am promoting in this volume (i.e., toward phylogenies as backbones, not proxies), and if more ecologists conduct clade-specific research, then a natural link with functional phylogenomics will be formed. Specifically, a major future direction should be to conduct functional phylogenomic analyses of clades and to use this information to link biogeographic history and functional evolution to understand the processes driving community assembly. Specifically, the species trees inferred can be used, as they have often been used, to infer the

biogeographic history of a lineage, including inferences regarding the importance of dispersal and vicariance. However, because the analyses produce functional gene trees and concordance and conflict can be measured, one would be able to quantify how these are related to biogeographic events or shifts in climatic niche space (e.g., Evans et al. 2008). For example, one will be able to search where in the phylogeny major climatic niche shifts or life-history changes have occurred and then identify the gene trees related that align with these events. Similarly, expansion of gene families can be investigated in the light of diversification rates across the clade, such that one may be able to investigate, for example, whether expansion in plant defense gene families coincides with rapid diversification and an increased probability of co-occurrence of closely related species.

A final set of future directions that I will discuss seeks to integrate information regarding differential gene expression and functional phylogenomic inferences. Over the past few years, ecology has begun to experience the integration of comparative differential expression studies from non–model organisms. Previous work had largely focused on differential expression in a single, often model, species. However, comparative studies are now financially feasible, and they will likely increase rapidly in the literature. A clear difficulty with such comparative studies is that it is not always clear what can or should be compared. I have discussed this issue earlier in this chapter, noting that most current studies compare gene set enrichment across shared gene ontologies, but not individual homologous or orthologous genes. Functional phylogenomics can facilitate such a study. Indeed, comparative differential gene expression studies may require a functional phylogenomic approach because, as I have described earlier, many genes are unannotated and therefore cannot be compared without a formal functional phylogenomic study.

Beyond being a methodological requirement, the integration of functional phylogenomic and differential expression studies could address several interesting questions. One of these questions is whether nucleotide similarity scales with expression similarity (Brawand et al. 2011; Yang and Wang 2013). There is surprisingly little information on this issue. The little that does occur at present in the literature indicates that sequence similarity is often a strong predictor of expression similarity across most tissues in plants and mammals. However, this scaling does not neatly hold when reproductive tissues (e.g., testes and flowers) are analyzed (Brawand et al. 2011; Yang and Wang 2013). These comparisons of tissue expression levels are interesting, but an ecologist may be as or more interested in how expression scales with nucleotide similarity in the context of environmental changes instead of different tissues. For example, it would be interesting to know if the interspecific correlation

between nucleotide similarity and expression similarity exists under normal and stressful conditions or whether species converge on similar expression "solutions" when under stress. In other words, does phylogenetic signal in expression found under normal conditions shift to antisignal under stress? Conversely, signal could be found under both conditions, and more distantly related species could simply have different approaches to dealing with stress.

Along these lines, analyses comparing sequence and expression similarity should be conducted in systems of closely related species. Most studies to date of this nature have compared very distantly related model organisms (e.g., rice, corn, *Arabidopsis*; Yang and Wang 2013). Is it that the signal found in these studies is simply due to the large taxonomic scale, or would nucleotide-expression correlations hold within genera as well? Such studies are needed, and they should be conducted not only comparing tissues, but comparing expression across different environmental stressors and documented physiological responses. These studies are likely still too costly to conduct in the field, due to the large sample sizes needed, but controlled experiments in the lab or greenhouse where genomicists and ecophysiologists work in collaboration would be feasible and valuable. All of this information would be incredibly useful for researchers attempting to determine how evolutionary history (i.e., phylogeny) influences ecological interactions.

A final reason why determining the relationship between interspecific distances on gene trees and expression similarity should be of great interest to ecologists is cost. The thin literature on this issue indicates that sequence similarity does predict expression similarity across most tissues. This is intriguing evolutionarily. However, it might also suggest that sequencing the transcriptomes of species and constructing gene trees may be "enough" for many ecological studies. In other words, the sequencing of biological replicates across two to many different environmental conditions could be eschewed, thereby saving the investigator a tremendous amount of money. I should say that I am skeptical that this will be the outcome once more data are accumulated, but I would be happy to be wrong, and the field should address this question as soon as possible. The cost of sequencing for differential expression could double to quintuple the cost of a typical contemporary study, and it would be nice to know if this cost is needed in most cases or not.

In summary, I find the integration of transcriptomics into ecology to be very exciting, and I think functional phylogenomic approaches will likely play an increasingly important role in this integration (Swenson 2012b; Swenson and Jones 2017). These approaches are conceptually and analytically critical, but I think they will also open up previously unimaginable avenues for phylogenetic ecology research. We will quickly transition from measuring a

handful of traits and mapping their evolution onto a phylogeny and toward assaying the tens of thousands of functional genes in a given tissue across species and tracing how the evolutionary history of these genes coincided with major biogeographic events and niche evolution. While functional phylogenomics is still a very young field and we have few examples of how this field has been integrated into ecology, I hope you have found the discussion in this chapter of interest, and that it will potentially inspire you to consider how transcriptomic information may be useful in your future research.

8

Building Trees for Every System and Scale and Biodiversity Informatics

Phylogenetic ecology, of course, depends entirely on the availability of phylogenetic trees containing the species in the systems of study. In the not too distant past, ecology was a landscape where only a few labs working on model clades could conduct detailed phylogenetic analyses, while the remaining researchers either avoided phylogenetic analyses or utilized information from the taxonomic hierarchy as a substitute. This situation has been rapidly transformed, to the point where a phylogenetic tree can be quickly generated for most study systems outside of microbes. This transformation to some extent has been driven by increasingly large databases, but to an even greater extent by informatics tools designed to catalyze phylogenetic ecology.

Here, I first discuss the recent advances that have made phylogenetic information available to ecologists across scales. Ideally, phylogenetic ecology would leverage a highly resolved tree of life. However, despite the optimism of some, I fear that such a tree is not likely to materialize in the very near future, as present sequence repositories are very sparse and taxonomically and spatially biased samples of the biosphere. Given this reality, alternative approaches and tools are necessary for estimating phylogenetic relationships that can be utilized in phylogenetic ecology. These approaches and tools have been generated, and they have catalyzed a large fraction of the phylogenetic ecology in the literature.

The informatics advances that have made phylogenetic information available to the world of ecology have come with a cost. Specifically, the phylogenetic inferences made are often of moderate to low quality or, in some cases, downright crude. The question, therefore, becomes whether the phylogenetic trees are "good enough" to address the questions researchers are frequently interested in addressing, and how sensitive to tree quality are commonly used

methods. In those instances where reconstructing the evolutionary history of traits or the biogeographic history of a lineage is paramount, such phylogenies will greatly hinder a study. Indeed, such investigations likely should not be conducted with the tools discussed in this chapter. However, in instances where quantifying phylogenetic diversity is the goal or the analyses are most heavily influenced by basal relationships, phylogenetic trees with multiple flaws may still be enough for reasonable inferences (e.g., Swenson 2009a). I will discuss this possibility in the chapter as well as the documentation of where phylogenetic quality and resolution have been shown to be important.

Next, I will discuss phylogenetic imputation methods, which are phylogenetic regression models that can be adapted to predict missing trait values upon the basis of assumed or measured phylogenetic signal. While these methods have existed for decades, they have not been utilized until recently (Swenson 2014b). The implementation of phylogenetic imputation methods on large sparse data sets is still nascent, but these methods may provide a pragmatic approach for gap-filling important global databases until additional data are collected in the future. I will discuss the major classes of phylogenetic imputation methods and discuss empirical evidence demonstrating their ability to predict missing trait data.

Finally, I end the chapter with some suggestions for novice researchers looking to integrate large phylogenetic trees into their research that will likely be derived from informatics tools. As the phylogenies in studies increase in size and simultaneously become easier to make, it will become very easy to make flawed inferences that may or may not be obvious. These problems are to be expected and will not be totally avoided or stopped, but they can be greatly mitigated through consideration of the suggestions I present.

8.1. A Tree for Every System

An initial impediment to the development of phylogenetic ecology, whether it was phylogenetically informed comparative analyses, measures of phylogenetic diversity, or analyses of community assembly, was a lack of phylogenetic information. This is not to say that systematic biologists were not working quickly enough or doing important work. Rather, ecologists frequently analyze taxonomically diverse samples from the tree of life. This means that even if a well-resolved phylogenetic inference for a clade in an ecologist's data set was available, it does not mean a phylogenetic tree for the other clades was available, nor was a phylogenetic tree that connected the well-resolved group to those other species in the ecological data set. In other words, phylogenetic ecology analyses typically demand a compilation of detailed basal and termi-

nal phylogenetic relationships that are not a primary output of a systematist focused on her or his favorite group.

Surmounting the first of these obstacles, which ultimately would mean generating a species-level tree of life, is a grand challenge for the biological sciences and underscores the increasingly underappreciated need for biodiversity exploration, broadening and maintaining biological collections, and training and funding more systematic biologists. There have been impressive advances made in this realm in recent years, with the Open Tree of Life and the Time Tree of Life being great developments (Hedges and Kumar 2009; Hinchliff et al. 2015; Hedges et al. 2015; Kumar et al. 2017). However, I would argue that we are still a long way off from a highly resolved, time-calibrated phylogenetic tree comprising all species from a kingdom, much less the planet. I am sure there are those that would disagree with this viewpoint. Such disagreements may be more likely from those studying only vertebrates or those that haven't spent enough time working in systems where the organisms encountered in the field cannot be quickly looked up in a field guide and many are still undescribed. There is a lot left on the planet to discover and describe, and assuming we will have it all incorporated into a detailed phylogeny in the next couple of years still seems foolishly unrealistic to me. However, I look forward to being proven wrong, and I hope that the perception that we can build trees of life using only the current information and taxonomic sampling does not take hold. A high priority still needs to be placed on collecting and sequencing specimens from diverse and/or underexplored regions and clades. In sum, this challenge is not so daunting if one works on vertebrates, but for the rest of biology it is still a challenge that cannot be pushed aside as something that has been solved or will be solved in short order.

The second challenge of providing phylogenetic information connecting taxonomically diverse species in an ecological sample is fundamentally different and more immediately solvable. The challenge is resolving and placing ages on the phylogenetic backbone or basal lineages of major clades. For example, this challenge has been tackled in plant biology by the Angiosperm Phylogeny Group (APG) (APG 1998, 2003; Bremer et al. 2009). The APG has played a pivotal and revolutionary role in the continued development of plant systematics, but the phylogenetic inferences produced by the APG have opened up the opportunity to estimate a phylogenetic tree for every angiosperm plant assemblage. Webb (2000) realized this opportunity while conducting his investigations of Bornean tree assemblages during his doctoral studies. Recall that Webb (2000) was building off the genus-to-species ratio literature that had been used to infer the drivers of community assembly over the previous 80 years. A problem with the genus-to-species ratio literature

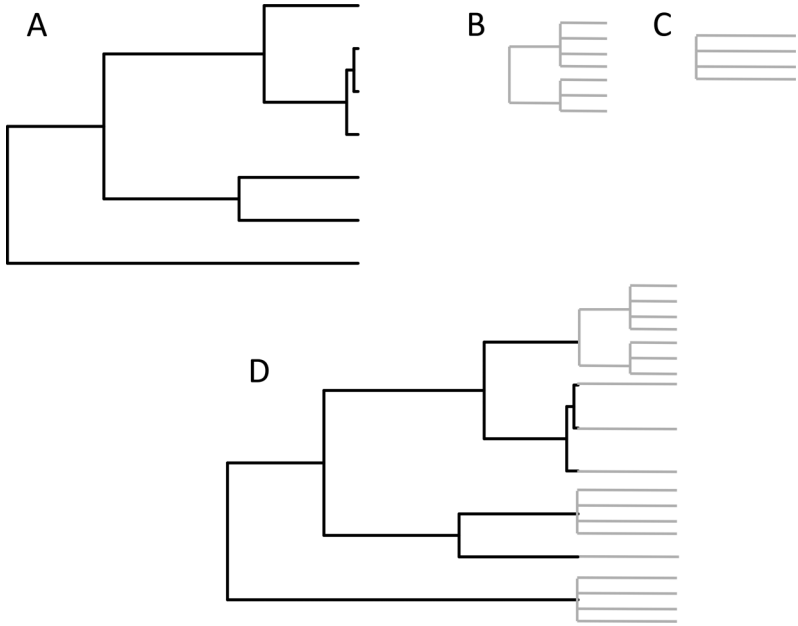


FIGURE 8.1. A hypothetical construction of a phylogeny of an assemblage (D) generated by assembling a "tree of trees." Here, a backbone phylogeny perhaps resolved to the family level (A) is then modified to include species using taxonomic relationships. For example, phylogeny B represents a family with two genera—one genus with four species and one with three. Phylogeny C represents a family with four monospecific genera. These topologies are pasted onto the backbone phylogeny to produce the community phylogeny.

recognized by Webb was that basal relationships were not represented, and these deep relationships may have ecological consequences. Webb's solution to this problem was to use the most recent APG phylogeny to estimate the basal relationships between the species in his communities that would ultimately allow him to calculate the phylogenetic distance between all species instead of a genus-to-species ratio.

The approach of Webb (2000) was soon enhanced to build what has been termed a tree of trees (fig. 8.1), where phylogenetic trees inferred for terminal groups or taxonomic hierarchies were appended to the basal topology (e.g., the APG phylogeny). The idea was that these large phylogenetic trees could be pruned to generate a phylogenetic topology connecting all species in a list provided by the user where terminal relationships were largely "resolved" upon the basis of the existing taxonomic hierarchy. What emerged was the informatics tool Phylomatic (Webb and Donoghue 2005), which arguably was one of the most important informatics advances in ecology over the past decade. Early versions of Phylomatic were only accessible online. Through

the use of downloadable affiliated software, Phylocom (Webb et al. 2008), users could use cladograms output from Phylomatic to (very) roughly estimate the ages of nodes and therefore branch lengths. More recent versions can be downloaded and used locally and seamlessly to go from a list of species to a phylogenetic tree within minutes. This tool alone nearly overnight changed phylogenetic ecology from being a somewhat small subdiscipline occasionally represented in the pages of ecological journals to a major research discipline now represented in a high fraction of the issues published in major ecological journals.

In recent years, more and more phylogenetic ecologists have used alternative methods for generating trees for their study systems, but the basic idea developed in Phylomatic still plays an important role. One example of this is the use of a Phylomatic phylogeny as a guide tree in phylogenetic inferences (e.g., Kress et al. 2010). Specifically, researchers can download DNA sequence information from a public data repository that is available for the species and DNA regions of interest. This often results in a sparse DNA data matrix with missing regions for some species and species with no available sequence information at all. A phylogenetic inference directly from this sparse matrix may produce clearly flawed topologies, and a Phylomatic guide tree may be used to constrain the reasonable inference space. Furthermore, for those species missing DNA sequence information, they may later be added to the phylogeny using the same approach as Phylomatic (i.e., attaching them to the node associated with their most terminal taxonomic rank). These tools are attractive, but they also bring ecologists firmly into the world of molecular phylogenetics. Previous work based only upon Phylomatic trees meant that fewer consequential decisions were being made by the ecologist during tree production. Newer informatics tools that download and align sequence information to ultimately infer a tree have many critical decisions being made by the user and/or by default. The push toward making these tools easy to use for ecologists may be coming at an immense cost. For example, when automated tools conduct important steps, such as multiple sequence alignment, in the background (phyloGenerator; Pearse and Purvis 2013), and these steps are not checked in detail by the researcher, dubious phylogenetic inferences may be common. The typical ecologist inferring large phylogenies may not take the time to check these steps carefully or know what they are looking at, which will lead to many questionable downstream results and inferences. In sum, it is unlikely that well-resolved, time-calibrated, species-level phylogenies for large (nonvertebrate) clades in a tree of life will be available in the near future. Thus, Phylomatic-like solutions will continue to be used, and

ecologists will need to retain a skeptical eye when assessing the quality of the trees produced and should not blindly use informatics software.

8.2. The Tree and Is It "Good Enough"?

The generation of phylogenetic trees for ecological studies during the past decade has been accomplished primarily through a Phylomatic-like approach. This gave rise to studies that have a phylogenetic tree and not a distribution of phylogenetic trees. Some ecologists may not have understood the importance of this distinction conceptually, but most have not attempted to perform analyses of any kind regarding the sensitivity of the result to the tree produced from a Phylomatic-like approach. This is despite the large number of polytomous nodes in a Phylomatic-like tree and the relatively crude approach for estimating node dates and consequently branch lengths. Thus, while there is indeed a single phylogenetic topology produced by informatics tools for phylogenetic ecology investigations, these topologies and their dating can be modified to estimate the sensitivity of the downstream results to these factors.

The lack of resolution between congeneric species and between genera within a family was a major criticism of early phylogenetic ecology studies. In response to several such reviews during my doctoral work, I decided to conduct a sensitivity analysis of popular phylogenetic diversity metrics utilized in community ecology (Faith's Index, mean pairwise distance, and the mean nearest neighbor distance) to phylogenetic resolution (Swenson 2009a). The study simulated phylogenies with known topologies and simulated community data as well across a broad range of parameter values (e.g., phylogenies with 20 to 320 species). Next, I used several approaches to reduce the quality of the original "known" phylogeny. First, starting from the most terminal internal nodes in the phylogeny, polytomies were introduced until 15%, 20%, 25%, or 30% of the original internal nodes were now included in a polytomy. Second, I unresolved 15%–30% of the phylogeny by randomly selecting nodes in the phylogeny instead of beginning with the most terminal nodes. The first approach was used to approximate a phylogeny generated by a Phylomatic-like algorithm where congeneric species were not resolved. The second approach was used as a null comparison to the first approach and as an example where phylogenetic uncertainty has no phylogenetic bias (e.g., within a particular clade or at a particular depth in the phylogeny).

The baseline expectation for studies that have phylogenies with more polytomies is that they will be biased toward the overestimation of phylogenetic

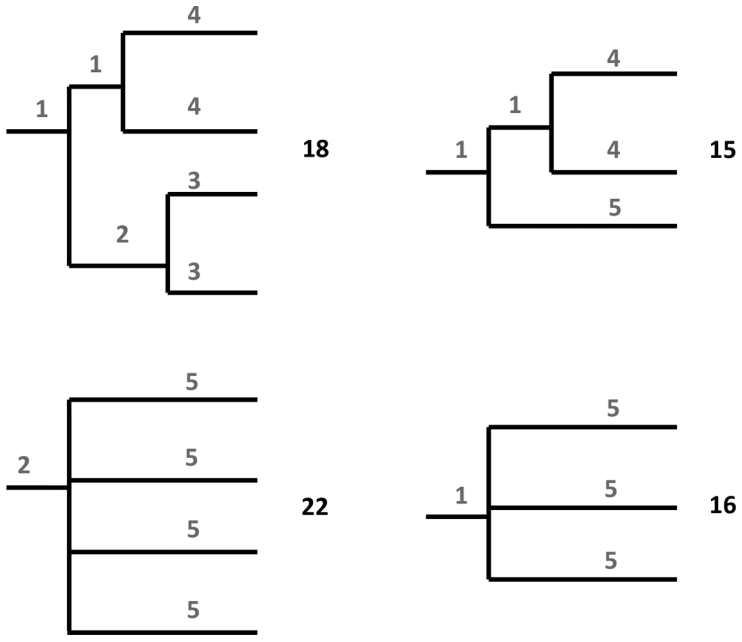


FIGURE 8.2. Two examples of how a lack of phylogenetic resolution can increase phylogenetic diversity. On the left, the top fully resolved phylogeny has branch lengths equal to 18, but if the basal-most node is unresolved, the total branch length is 22. On the right, the total branch length increases from 15 to 16 due to a lack of resolution. Thus, unresolved trees are biased toward overestimating phylogenetic diversity.

diversity (fig. 8.2). This is because the length of a stem branch to a clade is now doubled when a polytomy is introduced. This should be expected to be minimized when short stem branches are collapsed into polytomies, and when the phylogenetic diversity metric is a "terminal" metric like the mean nearest neighbor distance and not a more "basal" metric like the mean pairwise phylogenetic distance. However, these expectations were largely undocumented in the literature, and it was unclear whether these biases impacting observed phylogenetic diversity values would be removed or magnified when conducting a null modeling analysis.

The final analyses, which ultimately focused on biases in null model–based measures of phylogenetic dispersion, uncovered several important and consistent biases. First, the loss of basal resolution relative to terminal resolution had a far greater impact on phylogenetic dispersion metrics. This effect was magnified in smaller phylogenies, whereas on larger phylogenies the nearest neighbor metric was less sensitive to the random introduction of polytomies. Thus, if one has to utilize a phylogenetic tree lacking resolution for measuring phylogenetic diversity and dispersion, then less bias is intro-

duced if the polytomies are skewed terminally. In other words, a Phylomatic-like tree may not be as bad as some believe. However, a second key result from this work was that a lack of resolution in a phylogeny leads to standardized effect sizes that are closer to zero than what they should be if the "real" phylogeny was used. In other words, polytomies result in a bias toward incorrectly not rejecting the null hypothesis (i.e., Type II error; fig. 8.3). Thus, the phylogenetic community ecology literature, which was at that time almost exclusively using Phylomatic-like trees, was underestimating the amount of nonrandom phylogenetic structure in communities.

In the years that followed, fully (or nearly fully) resolved phylogenetic trees for communities began to be produced using sequence data in the form of DNA barcodes. The first such DNA barcode community phylogeny produced for the Barro Colorado Island (BCI) forest dynamics plot by Kress et al. (2009) was used to quantify biases in previous phylogenetic analyses of that tree community that used a Phylomatic tree. Specifically, Kembel and Hubbell (2006) had analyzed the phylogenetic dispersion of tree communities on BCI and related the degree of dispersion to habitat categories, generally finding weakly nonrandom or random results supportive of Hubbell's neutral

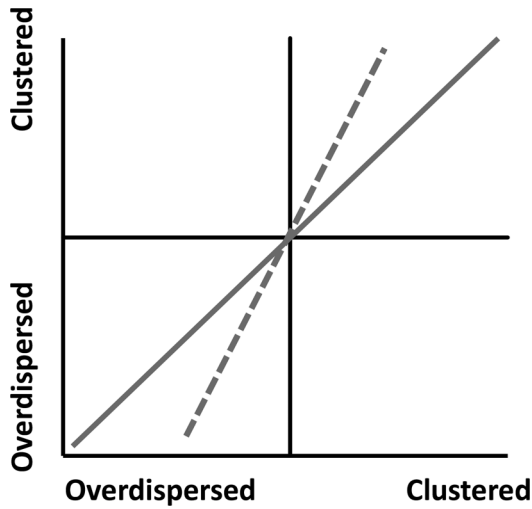


FIGURE 8.3. A cartoon of the results uncovered from simulation (Swenson 2009a) and empirical (Kress et al. 2009) studies showing how phylogenetic dispersion is sensitive to phylogenetic resolution. The solid gray line indicates the relationship between observed (*x*-axis) and expected (*y*-axis) values for a fully resolved phylogeny. The dashed gray lines are the values for a less resolved phylogeny. The solid black lines indicate null results, overdispersed indicates more phylogenetically diverse than expected, and clustered indicates less phylogenetically diverse than expected. Thus, unresolved trees tend to find values that are closer to the null expectation (i.e., higher Type II error rates).

theory (Hubbell 2001). Kress et al. (2009) repeated the same analyses using the same data except replacing the original Phylomatic phylogeny lacking terminal resolution with the resolved DNA barcode phylogeny. The change in results was consistent with that expected, given the simulation-based work by Swenson (2009a). That is, Kembel and Hubbell underestimated the degree of nonrandom phylogenetic structure in the BCI tree community by using a phylogenetic tree with a large number of polytomies. Kembel and Hubbell (2006) were using the best tree available at the time for their study and, therefore, cannot be criticized too greatly. However, it does serve as a cautionary note compelling phylogenetic ecology researchers to perform sensitivity analyses, if possible, when the phylogeny or phylogenies have clear limitations.

It is expected that imperfect, not fully resolved phylogenetic trees will continue to be utilized in ecology, and that these phylogenies will introduce biases beyond those now known for measures of phylogenetic diversity. For example, recent work by Davies et al. (2012) has demonstrated that polytomies increase the bias toward estimating phylogenetic signal using Blomberg's *K* statistic (Blomberg et al. 2003). This is not unexpected, as an unresolved phylogeny underrepresents the amount of shared branch length between species, and therefore any similarities in traits between taxa seem more exceptional given the perceived lack of shared branch length (i.e., nonindependence) (fig. 8.4). Importantly, if one is conducting one-tailed tests of signal instead of two-tailed tests for signal or antisignal, then the Davies et al. (2012) work indicates a lack of resolution results in elevated Type I error rates for the *K* metric. In other words, a lack of phylogenetic resolution will not affect error rates in the same manner across all phylogenetic analyses, and we cannot simply assume that the results from one article regarding one metric apply to all other metrics.

A reasonable approach for dealing with issues related to polytomies that are frequently found in phylogenies generated by informatics tools is to perform sensitivity analyses where the unresolved relationships are randomly resolved and the downstream analyses repeated several hundred or thousand times to generate a distribution of possible results (Donoghue and Ackerly 1996; Rangel et al. 2015). This approach, while attractive in that it directly demonstrates the magnitude of bias, is not without its own faults. First, the number of ways to randomly resolve the topology of a given phylogeny can be astronomical, not to mention the nearly infinite distribution of possible branch lengths. Thus, it is not possible to explore even a modest fraction of possible resolved tree space. Second, nonrandom processes generating lineage diversification could mean that the "real" result is found in the tails of

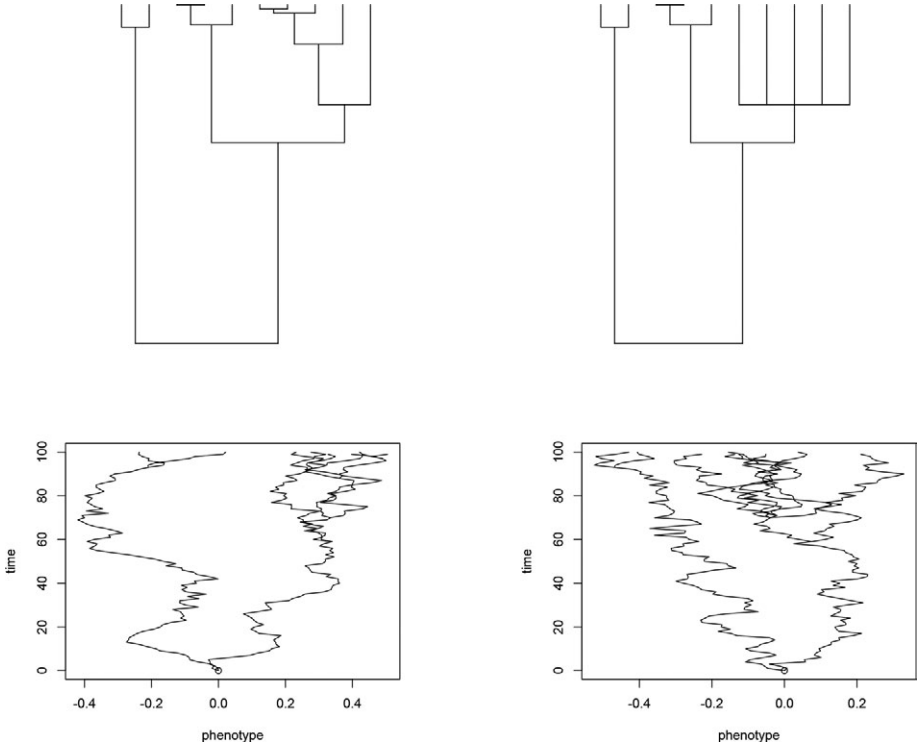


FIGURE 8.4. An example of how a lack of resolution may impact expected trait diversity. The top panels are the phylogenies, and the bottom panels are simulations of Brownian motion trait evolution along branches. On the right, a single clade has been polytomized. We can see that the phenotypic variance within the polytomized clade is higher, due to more independent evolution (i.e., branch length). On the left, there is more shared evolutionary history in the resolved clade and less variation in the trait values (i.e., less variation on the *x*-axis).

the distribution of possible results (i.e., not included in the 95% confidence intervals around the expected result). This could lead to a systematic bias layered on top of how we estimate bias in phylogenetic ecology. These issues with sensitivity analyses should be appreciated, but I would argue that not attempting to estimate bias while discussing the limitations of the sensitivity analyses used is a far worse option than relying on the result from a highly unresolved tree alone. I am sympathetic to the fact that there are some instances where the size of the phylogeny or complexity of the analyses being used may prevent or limit sensitivity analyses, but these cases are rarer than the literature indicates (i.e., the number of articles not performing sensitivity analyses regarding resolution).

The above discussions revolve around the situation where a phylogenetic ecologist has access or can generate only a single phylogenetic tree from an

informatics tool. This was generally the case in the early 2000s. However, ecologists increasingly are using sequence data to generate phylogenies for their study species de novo. In so doing, a distribution of phylogenetic trees can be inferred that may be equally likely or indistinguishable in their quality. A consensus phylogenetic tree may be generated from this distribution of trees. Alternatively, the researcher may simply select one of these trees from the distribution and use it for downstream analyses. A consensus tree has the major downside of typically not having branch lengths or having to make questionable decisions about how to assign branch lengths (Felsenstein 2004). The second approach has the major downside of sampling one from a distribution (i.e., $n = 1$). Again, while not perfect, sampling many trees from a distribution and repeating the downstream analyses to generate a distribution of possible results would be advised (e.g., Evans et al. 2008). This is an approach that is not foreign to evolutionary biologists, but it does appear to be rare in the phylogenetic ecology and should be implemented much more frequently.

In summary, the development of informatics tools and DNA sequencing technology has set the stage for making phylogenetic information more accessible than ever for ecologists. When biologists infer phylogenies, it is generally understood that they are not stating that we know the "real" phylogenetic tree linking our study species (i.e., it is a work in progress or currently the best-supported hypothesis). In phylogenetic ecology, we are also confronted with the knowledge that our phylogenetic trees are often not up to the standard of a typical phylogenetics study. The phylogenies are often cobbled together from disparate and incomplete pieces of information, and may often be thought of as very crude by researchers focusing exclusively on inferring phylogenetic trees. Thus, phylogenetic ecologists are making the best of a bad situation where they are trying to at least roughly represent and quantify the evolutionary nonindependence in their data rather than completely ignore it. Does that mean that these often-crude phylogenies are good enough for ecological work? This is a question that has not been well addressed, and more attention must be given to addressing it going forward, as phylogenetic uncertainty is not a problem that will go away. In addressing this issue, more thought should go into the process one is trying to elucidate or the problem they are trying to solve. Crude phylogenetic trees being used to provide rapid estimates of phylogenetic diversity for large nature reserves are likely to be good enough, given that fully resolved phylogenies will arrive after the nature reserve might disappear. Additionally, the practitioner should understand that critical real-world decisions should not be based only upon one potential reserve having two million years more evolutionary his-

tory and 900 species versus another having two million years less evolutionary history and 950 species.

Conversely, for those mapping trait evolution and biogeographic history onto phylogenetic trees to infer the assembly of biotas, typical phylogenetic ecology phylogenies generated from easily implemented informatics tools are not good enough, and even work based on highly supported molecular phylogenies would be substantially improved or even overturned with fossil evidence and the inclusion of extinct lineages. Thus, the field of phylogenetic ecology has grown due to the development of widely used informatics tools via the truly outstanding contributions of a few, but phylogenetic ecologists need to continue to confront uncertainty represented in these phylogenies by conceptually and quantitatively assessing how biased the results could be or not.

8.3. Phylogenetic Imputation: An Underappreciated Biodiversity Informatics Tool

The nonindependence of species due to their common descent leads to the expectation that closely related species will be more similar to one another than distantly related species (Felsenstein 1985). As has been pointed out throughout this book, this assumption is often violated, and when possible one should quantify the amount of phylogenetic signal in the data set of interest. Ecology has experienced the rapid development of informatics tools and approaches for inferring large phylogenies and large trait databases. The most-concerted efforts to this end have been in plant biology. This infrastructure and the grappling of community phylogenetics with the phylogenetic proxy assumption have resulted in a large number of studies reporting the amount of phylogenetic signal in trait data using data sets ranging from very local-scale to global. During his synthesis and discussion of this emerging literature, Donoghue (2008) noted that a surprising outcome is the large amount of phylogenetic signal in trait data related to ecological interactions. These ecological characters had been frequently avoided by systematic biologists in the past inferring phylogenies upon the basis of morphological traits. This avoidance was due to the belief that traits related to ecological interactions may be so evolutionarily labile as to not have enough signal for robust phylogenetic inference. Thus, one of the important conclusions being drawn by Donoghue (2008) is that traits related to ecology have more phylogenetic signal than one might expect, and this is why there is a strong phylogenetic imprint on ecological data sets when we look for it.

The surprising amount of phylogenetic signal in trait data discussed by

Donoghue (2008), of course, is one of the foundational arguments for the proxy-based approach to phylogenetic community ecology. A problem with this is that phylogenetic signal in traits distributed on global-scale phylogenies is prevalent, but within particular clades or geographic locations where a global context is not considered, the signal disappears (e.g., Cavender-Bares et al. 2009; Swenson 2011a). For example, two species in the palm family may appear to be very different in their traits, but when compared to a grass species they seem more similar to one another than they are to the grass. Thus, if we are interested in comparing the intricacies of very closely related species, phylogenetic information may not be valuable. However, if we are interested in roughly estimating the differences between distantly related species, then phylogenetic information may be very useful. With this in mind, it is worth considering how phylogenetic information may be used to help address grand challenges facing the biological sciences.

Many of the grand challenges facing ecologists demand the synthesis and analysis of big data. Consequently, ecologists and biodiversity informaticians have put considerable resources into generating global databases for variables related to species distributions, climate, and traits. These databases have improved and broadened the scope of ecological research, but the databases are also typically very sparse. For example, the largest plant trait database contains >50 traits and 148,000 taxa, but the matrix itself is almost completely empty, and nonrandomly so, with only a few traits and geographic regions comprising the majority of the data available (Kattge et al. 2011). Similarly, geo-referenced species occurrence databases, while improving, are notoriously patchy. During the late 1990s to today, species distribution models have been used to estimate the geographic distribution of species given their known locations and some environmental variables. This has been, in effect, a large exercise in gap-filling data. Suffice it to say that species distribution models are controversial, and even among those in favor of using them, there are strong disagreements in how they should be implemented. Particularly worrying is the application of these models to project the future distribution of species under a changing climate. However, species distribution models serve as really the only currently feasible and pragmatic way to provide somewhat reasonable estimates of present-day species distributions, given the reluctance to fund future collecting expeditions and the rapid destruction of our planet.

Gap-filling trait databases has received far less attention than the tremendous effort put into gap-filling spatial distribution databases. An obvious starting point is gap-filling trait databases through the reliance on trait correlations or functional syndromes. Plant functional ecology has identified

a handful of functional trait spectra or economics spectra where a suite of traits that are highly correlated define where a species lands along a global continuum of ecological strategies. For example, leaf nitrogen, specific leaf area, leaf photosynthetic rate, and leaf life span are all strongly correlated. These correlations may allow one to predict values for three of the traits with reasonable accuracy if the value for one trait is known. While the methods that exist for gap-filling or imputing data are slightly more complex than simple regression-based predictions, strong covariation between variables is a foundational concept in attempts to impute trait databases. In some cases, such as in the medical sciences, where strong allometries exist and data matrices are not terribly sparse, imputing trait data is reliable. In ecological trait databases, where trait covariation is not as strong and databases are much sparser, the ability of classic imputation approaches to predict trait values has been unclear.

Recent attempts to impute missing trait values in large sparse plant trait databases have provided the answer regarding whether trait covariation alone can provide reliable estimates. It cannot. An interesting outcome of this work, however, has been that introducing the taxonomic hierarchy into imputation approaches yields dramatically better and highly accurate trait predictions (Schrodt et al. 2015). In other words, reliable trait imputation upon the basis of trait covariation in supersparse global trait databases was impossible until crude information regarding the taxonomic nonindependence of taxa was introduced into the model.

In parallel with the development of imputations that used a crude taxonomic hierarchy has been the development of phylogenetically based imputation methods. The implementation of these methods was driven a priori, with the knowledge that species are not independent and that phylogenetic signal in global trait databases is common (e.g., Moles et al. 2005; Swenson and Enquist 2007). These approaches permit the use of phylogenetic branch lengths, which greatly refines how evolutionary nonindependence is represented over using taxonomic groupings (e.g., families), which vary tremendously in their ages. In some cases, they also allow for fitting models of trait evolution, given the observed data or variation in the rate of trait evolution between clades, and all methods can incorporate known levels of trait covariation and provide estimates of uncertainty. Phylogenetic imputation methods, therefore, hold tremendous potential for pragmatically imputing global trait databases, and testing and developing new methodologies merits much more attention (Swenson 2014b). In the following, I briefly describe some of the existing methods for phylogenetic imputation and how they have been implemented in recent work.

I will focus on two main classes of phylogenetic imputation methods. They are both derived from phylogenetically informed regression techniques discussed in the context of comparative methods in chapter 2. Phylogenetic generalized least squares (pGLS) regression is the first method that I will discuss. Recall that in pGLS there is a phylogenetically informed error, and this generally takes the shape of a phylogenetic variance-covariance (pVCV) matrix. The pVCV matrix, if Brownian motion trait evolution is assumed, has off-diagonal elements representing the shared branch length between sets of tips (e.g., heterospecific pairs of species) and diagonal elements representing the distance from a given tip to the root of the phylogeny. Thus, regressing a trait onto a value of 1 with a pVCV error matrix built upon a Brownian motion assumption gives a rough estimate of the strength of phylogenetic signal in the trait data via the r^2 value. This model could be constructed, for example, using seed trait data for 8,100 species. A goal might be to estimate the seed mass value of a set of 13,000 species. The r^2 of the original model, constructed using a pVCV matrix containing the 8,100 species, may give some insights into whether this is a reasonable goal using phylogenetic information. The acceptable variance explained is dependent on the researcher, but let us say for example that we are comfortable using a model that explains 80% of the variation for prediction. If the model meets these criteria, we could apply it to a pVCV matrix containing all 13,000 species. If the original model did not meet a certain criterion of variance explained or one would like to improve it even if the criterion was met, additional independent variables could be added. For example, if the seed trait is strongly correlated with the average temperature of the species range or with plant size and this information is available for species without seed trait data, the new independent variables can be entered into the model, and this model can be used to impute values for those species in the 13,000-species data set without seed data.

A downside of the pGLS approach just discussed is that it assumes Brownian motion trait evolution to generate the pVCV. As we discussed in chapter 2, this assumption can be avoided, and maximum likelihood can be used to fit the pVCV to the trait data. For example, if a λ transformation of 0.87 of the pVCV matrix fits the trait data the best in the original regression model, this λ transformation can be applied to the off-diagonal elements of the larger pVCV matrix when imputing missing trait values. This model is just as easy to apply as models assuming Brownian motion, and the flexibility afforded is a great benefit, as few traits ever have a λ of 1.

The other class of phylogenetic imputation methods that I will discuss are phylogenetic eigenvector based. These methods are regression models where the principal component axes derived from a principal component analysis

of a phylogenetic distance matrix are used as independent variables and the trait data is the dependent variable. Critiques of this approach include that it doesn't have a specified model of trait evolution and eigenvector selection methods may be dubious (Freckleton et al. 2002). However, as noted in chapter 2, eigenvector selection methods have been studied in more detail, since these initial critiques and whether a given model of trait evolution is explicitly specified or not is, perhaps, not of immediate concern to a researcher attempting to impute trait values in a global database. A clear benefit of the eigenvector method is that it breaks the phylogeny down into scales of information such that different magnitudes of phylogenetic signal at different depths or across clades in the phylogeny can be incorporated into the imputation model. Conversely, the pGLS methods just discussed apply a single λ transformation or value across the entire phylogeny, such that phylogenetic signal is consistent in strength across the phylogeny. Thus, eigenvectors might prove valuable due to their increased flexibility. Finally, as with pGLS methods, eigenvector models could also be improved by adding additional independent variables such as climatic data or other covarying trait data to strengthen the imputation.

There have been multiple published studies that have used phylogenetic imputation to gap-fill large databases. Almost all of these studies have sought to impute the values of very few species relative to the size of the database used to generate the original statistical model. There have been fewer studies imputing for a relatively large number of species, despite the fact that such large-scale imputation may be necessary for many pressing challenges in the ecological and environmental sciences where the vast majority of the data matrix may be empty.

In 2014, I started to explore whether phylogenetic imputation methods might be able to suitably gap-fill trait databases and be used to map the distribution of functional diversity (Swenson 2014b). To begin, I used what may be considered a taxonomically best-case scenario, where the empty cells in the trait matrix were closely related to other species in the trait matrix with data. Specifically, from other work with collaborators, we had compiled range map and trait information for trees in Europe and eastern North America (Swenson et al. 2016). Next, I removed all trait information for North American species from the trait matrix and attempted to impute this missing information only using European trait data and phylogenetic relatedness information. I also performed the reverse experiment—predicting Europe upon the basis of North America. The predicted trait values were then used to reconstruct the distribution and diversity of plant traits across Europe or North America. The phylogeny used for this study was generated by Phylomatic,

and therefore lacked a great deal of resolution within genera. I utilized pGLS fitting a pVCV and using a Brownian motion pVCV, as well as phylogenetic eigenvector models, so that I could compare approaches.

To my surprise, phylogenetically imputed trait values were very good representations in many traits, and strong predictions of the spatial distribution of trait values and functional diversity were possible (Swenson, Weiser, et al. 2017). For example, over 80% of the variation in seed mass distributions and over 60% of the variation in functional diversity across Europe could be recovered by phylogenetic imputation of trait values solely upon the basis of North American species values. No covarying traits or climatic information was used during the imputation process, suggesting that the models could be further improved.

There were, however, instances where phylogenetic imputation clearly failed. The study included at least one trait that is known to be evolutionarily labile—maximum tree height. The spatial models of maximum tree height across Europe and North America explained only slightly more than 10% of the known variation in the distribution of this trait. This result was roughly consistent across metrics, indicating that even the more flexible pGLS with a fit λ and eigenvectors could not be used to predict this labile trait. It is unclear how much these models could have been improved by adding other independent variables. For example, maximum tree height is typically correlated with temperature and precipitation values and, more importantly, their interaction. Thus, adding these variables may have greatly improved predictions. However, it is clear that some traits will be very difficult to reliably impute. In those cases where the model cannot be independently tested, the researcher would be wise to consult the phylogenetic ecology literature documenting the degree of phylogenetic signal in the trait or by checking the λ value in their own data. In cases where λ is low, one may decide that a phylogenetic imputation with no additional independent variables is unwise.

A second interesting outcome of the study was the asymmetry in predictive power across the two continents. The tree flora of Europe is much less diverse than that in eastern North America. This diversity anomaly is in part described by more congeners in eastern North America, but primarily due to several genera not found, at this point in time, in Europe. In other words, the tree flora of Europe is almost completely taxonomically nested inside that of eastern North America. This taxonomic nestedness resulted in asymmetric strength of results such that predictions of Europe will generally be stronger than predictions of eastern North America. Specifically, this occurs for two reasons. First, the functional space occupied by shared genera across the two continents is roughly equivalent (Swenson et al. 2016). This

is important because the addition of more species in a genus and therefore branch length will increase the expected functional diversity, but in reality, shared genera are not more functionally diverse in eastern North America than in Europe. Second, imputation of clades outside the phylogenetic range of the training data set used to build the model will lead to greater prediction error. For example, the *Magnolia* species in eastern North America may be outside the phylogenetic range of species in an angiosperm-based imputation based upon the European tree flora. This underscores the importance of the breadth of taxonomic or, more importantly, phylogenetic sampling used for imputation. A reduced breadth will increase the phylogenetic extrapolation, and may result in impossible trait values, particularly if no other independent variables are utilized to help constrain the imputation.

We compared the relative performance of the three imputation approaches used in the study. The best predictions were made by pGLS when fitting a λ to the observed trait data. However, this approach only marginally improved the predictions of a pGLS where λ was set to 1 (i.e., Brownian motion). The eigenvector method had the worst performance of the three, but in most cases the performance was highly similar to that of the other two. Thus, for the given data sets analyzed, we found that all were roughly equivalent, and major differences in predictions would not arise based upon the method utilized.

Finally, while not published in our original work (Swenson, Weiser, et al. 2017), we did investigate the impact of phylogenetic resolution on imputation. Specifically, we randomly resolved the polytomies in the phylogeny 100 times and reran all imputation analyses. We found that the analyses were relatively insensitive to polytomies. A polytomy decreases the actual shared history (i.e., covariance) between species pairs. We therefore expected that we would overestimate functional diversity, as there would be an overestimate of the time since divergence between species and therefore more time for trait values to diverge. The decreased sensitivity to polytomies may have been specific to our study, where there were very few genera with more than three species (e.g., *Quercus*) and few polytomies basal in the phylogeny. In other words, the amount of lost phylogenetic covariance was minimized. Studies lacking more basal resolution or containing many genera with more than three species would likely be much more sensitive to polytomies.

Moving forward, phylogenetic imputation methods will need increasingly rigorous tests. As mentioned, the evaluation described above was designed to approximate a best-case scenario where the species used to generate the statistical model were closely related to the species being predicted. Furthermore, the training and test data sets were from similar climates, such

that congeners that have colonized new climates and therefore may have undergone substantial trait evolution were not considered. Simulation studies should be one approach to testing the validity and reliability of imputation methods. Simulation studies have now been carried out to compare metrics, computational speed, and the fitting of evolutionary models to the data (Goolsby et al. 2017). Such studies are valuable, but more are needed. For example, it would be extremely valuable to have a simulation study that varied the degree of phylogenetic signal in traits, the degree of trait covariation, as well as the size and shape of the phylogenies used. More complicated simulation experiments may also vary the bias in the taxonomic sampling in each data set, to begin to get an idea regarding what is essentially phylogenetic extrapolation versus interpolation and whether any metric is a superior performer in such instances.

Similarly, more tests and comparisons of phylogenetic imputation methods using empirical data sets would prove valuable. For example, Penone et al. (2014) compared different imputation methods that did not require phylogenetic information and then included phylogenetic information to test relative performance. They concluded from their analyses that phylogenetic information generally improves the quality of imputation. However, this test focused on primarily allometric relationships; additional tests on traits not known to covary so strongly would be useful, as would tests using empirical data where portions of the data set were removed in a biased fashion. In sum, we need to now simulate purely using computer simulations or using deconstructed empirical data sets the worst-case imputation scenarios to determine whether imputation methods can be used for the types of super-sparse matrices found throughout ecology.

8.4. Conclusions

Phylogenetic ecology is at a point where it almost always demands the construction of large phylogenetic trees. The rapid development of informatics tools has sought to meet this demand, and has been the key catalyst in the rapid rise of phylogenetic ecology over the past two decades. As the trees get larger, informatics tools become more complex, and the scale of the ecological questions increases, it will become more difficult for the typical ecologist to become well versed in all aspects of the study. In other words, it will become increasingly challenging to address, with authority, what assumptions were or were not made during phylogenetic inference, whether phylogenetic inference is of high quality generally speaking, whether the phylogenetic inference

is "good enough" for ecological work, and whether the phylogenetic information is actually useful for the hypotheses of interest. I will, therefore, offer some humble advice to those embarking on a phylogenetic ecology project that relies on large phylogenetic trees and/or informatics tools.

First, become familiar with at least the basics of phylogenetic inference. Do not simply take the phylogeny given to you by another researcher or a program and run complex statistical analyses on it. Ask how the inference was made, what subprograms or modules were used in the inference pipeline, and how any of this may have impacted the phylogeny that is now in hand. Run some sensitivity analyses and compare the inferences using alternative and reasonable assumptions.

Second, to the best of your ability, look at the phylogeny! A general rule of thumb with any data is to plot it. A phylogeny is no different. Unfortunately, large phylogenies are notoriously difficult to visualize, but a little patience and effort will be rewarded. Does the topology approximate that suggested by systematists? If not, why? Previous topologies are hypotheses, as is yours, so they need not match perfectly, and we may expect that they often won't. However, major differences in topology should be an indication that some additional thought and analyses are needed prior to using this phylogeny in downstream analyses. Similarly, are your taxonomic groups monophyletic in the phylogeny? There may be good reasons for this (e.g., they are truly not monophyletic) or more insidious issues (e.g., mislabeled or misidentified specimens). Too often we are tempted to take a phylogeny for granted and move forward.

Third, collaborate with a systematist or phylogeneticist when possible. Collaboration with a systematist is particularly valuable, for obvious reasons, for clade-focused research using the phylogeny as a backbone instead of a proxy for similarity. A systematist will know the group you are studying in far more detail than you will ever know it; they will be able to quickly identify places where the phylogenetic inference looks suspect; and they will be familiar with the distribution of the lineage through space and time. If you are simply using a large phylogeny to quantify phylogenetic diversity or using it as a proxy for more similarity, you are probably using a phylogeny composed of so many taxonomic groups that it likely will be beyond the scope of interest for many systematists. However, a phylogeneticist focusing on reconstructing large trees would be invaluable as a collaborator, as they will be able to assure the quality of the phylogenetic inference. While collaborations are not always perfect and can be, in some cases, a total disaster, they are a necessity as our analyses become more integrative and multidisciplinary.

Finally, perform sensitivity analyses. A distribution of phylogenetic trees

is almost always produced, and when computationally possible, which is almost always, one should run the analyses on a large sample of this distribution. A researcher can then present a median and confidence interval around the parameters they are trying to estimate. If a single phylogeny is produced, for example in the case of a Phylomatic tree, the phylogeny likely will have soft polytomies. These can be randomly resolved multiple times, and analyses can be rerun to assess sensitivity. Ecology needs to get more in the habit of producing phylogenetic sensitivity analyses, and this will become even more important as phylogenies increase in size.

9

Conclusions and Remodeling Phylogenetic Ecology

The use of phylogenetic information in ecology is widespread (Cavender-Bares et al. 2009). It is no longer restricted to something that may cause nonindependence in data sets. Rather, phylogenies have become important tools in the toolboxes of those studying comparative ecology, conservation biology, community ecology, and macroecology. While the use of phylogenetic information in ecology has become somewhat normalized, a spectrum of acceptance exists along which researchers fall. From my interactions with colleagues, I suspect the distribution of ecologists along this spectrum is bimodal, with those that are incredibly enthusiastic or incredibly pessimistic about phylogenetic ecology. Neither of these perspectives is reasonable, and I hope the readers of this book have come to a similar conclusion.

The perspective outlined in this book is that phylogenies are not a magical cure for all that ails ecology, nor are they part of some passing fad or bandwagon. Rather, they are useful in many instances and less than useful in other instances. Furthermore, I have argued that phylogenies are, at present, often utilized in ecology in ways that do not maximize their power and are, in some cases, used in a way that will lead to flawed or very incomplete inferences. Some of this is due to the legacy of how relatedness has been used in ecology. Some of it is due to a lack of detailed phylogenetic information. Finally, some of it is due to a failure to seriously consider the impacts of evolutionary and biogeographic history on present-day ecological outcomes.

Here, by outlining the historical development and emerging concepts and tools in phylogenetic ecology, I have aimed to rationalize why the field has ended up in its current state, and to highlight how the course can be adjusted to maximize the utilizes of phylogenies in ecology. The course adjustment or remodeling in phylogenetic ecology should begin with five foci I intro-

duced in chapter 1. In subsequent chapters, I filled in historical detail and context, such that we can now return to these five foci. In each of the following sections, I reiterate one of the foci and make recommendations for what research paths or decisions may be more fruitful than others. Following this advice won't always be simple or possible, but I hope it provides a reasonable road map to a future phylogenetic ecology that strongly integrates evolutionary history into ecology conceptually and analytically.

9.1. Phylogenetic Signal Should Be Quantified and Incorporated into Ecological Analyses

Phylogenetic signal can be defined as the degree to which the shared evolutionary history of two species explains their similarity in a given trait (Bomberg and Garland 2002; Bomberg et al. 2003). Thus, two species do not have to have identical trait values for there to be phylogenetic signal in the traits. We contrasted this with phylogenetic trait or niche conservatism *sensu stricto* (Swenson 2011a), where there is no trait or niche difference between the two species. Phylogenetic conservatism is of interest and relevant to the phylogenetic ecology literature (Wiens and Graham 2005; Wiens 2008: Cavender-Bares et al. 2009), but it is not the focus here. Rather, we are focused on the measurement of phylogenetic signal and the application of this signal in ecological analyses.

Defined another way, phylogenetic signal indicates the degree of phylogenetic nonindependence in a variable. This signal may be assumed a priori, as we have seen in some of the comparative methods described in this book. Typically, this has taken the form of a phylogenetic variance-covariance matrix (pVCV). Recall that the off-diagonal elements of the pVCV indicate the amount of shared branch length between two tips and, therefore, the expected amount of trait covariance given a typically Brownian motion model of trait evolution. The diagonal elements of the pVCV indicate the root-to-tip distance for a given tip and, therefore, the expected variation in a trait given a Brownian motion model of trait evolution assumption. Specific examples of the Brownian motion model and pVCV in this book include the phylogenetic generalized least squares (pGLS) regression and a special instance of the pGLS called phylogenetic independent contrasts. We have also seen the Brownian motion and the pVCV utilized to quantify the phylogenetic diversity of a community (Helmus et al. 2007). Thus, phylogenetic signal is often assumed in analyses.

I have also described instances where phylogenetic signal is estimated given the trait data and the phylogeny. For example, we have discussed Blom-

berg's *K* statistic (Blomberg et al. 2003) and Pagel's λ (Pagel 1999) as being two of the most widespread measures of phylogenetic signal in the phylogenetic ecology literature. Furthermore, we have discussed pGLS where a λ transformation of the pVCV is estimated with maximum likelihood for comparative analyses or phylogenetic imputation. Other work in evolutionary biology, discussed in less detail in this volume, focuses on competing alternate models of trait evolution to determine which fits the data best.

Thus, we have two complementary, but somewhat different, approaches to phylogenetic signal in the literature: those that assume a purposefully simplistic or agnostic model of trait evolution and those that attempt to fit one. Both of these approaches have their place in the literature. Admittedly, the assumption of Brownian motion is simplistic and many have a strong desire to move past this simple assumption, and some may even consider the simplicity of it enough to disregard phylogenetically informed comparative analyses. However, in some instances, it serves as perhaps the only reasonable way in which to include phylogenetic information in a study. For example, in those instances where no trait information is available, Brownian motion and the associated pVCV serve as a conservative expectation for how phylogenetic relatedness may impact a system. Such instances would include the measurement of phylogenetic diversity in communities where no trait data are available. This is explicitly done using Helmus's *PSV* metric (Helmus et al. 2007), and the direct relationship between the pVCV and a phylogenetic distance matrix indicates that it is also explicitly done in all distance-based measures of phylogenetic alpha and beta diversity (Swenson 2014a). Cases such as these are not common in present-day phylogenetic ecology, and there is uncertainty regarding what the results actually mean. Thus, a simple assumption of phylogenetic signal should be accepted less and less, and it will likely serve primarily as a starting point for method development rather than an assumption in an actual analysis.

The other option of directly measuring the degree of phylogenetic signal in the data should be the more commonly used approach. There are many reasons for why phylogenetic signal should be measured and not assumed, and some of these are nicely outlined by Losos (2008, 2011). One major reason for measuring signal is that it might be weak or nonexistent. This is particularly important for those studies that utilize relatedness or measures of phylogenetic diversity to draw ecological inferences or set conservation priorities. While researchers have found a surprising amount of phylogenetic signal in large ecological trait data sets (Moles et al. 2005; Swenson and Enquist 2007; Donoghue 2008; Swenson, Weiser, et al. 2017), the degree of signal varies among traits, and there are well-known examples where strong

convergence in traits or niches has been demonstrated (Losos et al. 1998; Gillespie 2004; Cavender-Bares et al. 2004). Furthermore, there is likely a strong scale dependency in phylogenetic signal, such that it may not be evident if one only investigates closely related species. After all, sister species almost certainly diverge in some manner ecologically (Sobel et al. 2010). These divergences, however, may appear relatively small if one is studying, for example, all angiosperms instead of a single genus (Swenson 2011a). In sum, traits vary in their signal, signal is frequently not found, and signal may often depend on the taxonomic scale of the study (Cavender-Bares et al. 2009). For these reasons alone, phylogenetic signal should be measured whenever possible. Beyond these reasons, phylogenetic signal should be measured in any comparative study prior to downstream analyses. If there is no or weak phylogenetic signal, then that phylogenetically informed metrics could, theoretically, be avoided. However, this approach is not advised, as incorporating phylogenetic information into an analysis (e.g., using pGLS) will often lead to additional insights. Thus, measuring phylogenetic signal when trait data are available is a recommended first step.

The measurement of phylogenetic signal, though, should not be an endpoint or final goal of the investigation. This information should then be applied and placed into context. One example of this is simply to quantify the signal in data (e.g., λ), and to directly incorporate this into the comparative analyses (e.g., pGLS) downstream. The interpretation of this signal in many cases in phylogenetic ecology should stop at this point. That is, if no phylogenetic signal is found in a trait in a shrubland community someone studied, that should not be interpreted in an evolutionary context unless under very special circumstances. This is because the phylogenetic sample (i.e., the community) is often a nonrandom paraphyletic sample of a tiny fraction of the tree of life. Thus, there is little that can be learned about the tempo and mode of trait evolution from the data in a single community. Similarly, one should not cite a measure of phylogenetic signal in a community and state that it has been shown that the trait has signal, generally. The only circumstances where this general rule may be misguided are those cases where the community is a single clade or full of clades that are very densely sampled. In such instances, the tempo and mode or signal in trait evolution within those clades would be of interest.

The detection of phylogenetic signal or a lack of signal will be of general interest when the study is conducted using densely sampled phylogenetic trees and, therefore, most likely when a study is conducted on large spatial scales. This would provide useful insights into the evolutionary history of the trait, but downstream analyses are still necessary. For example, one should

ask whether the signal is consistently strong across the clades in the phylogeny and, if not, what causes this inconsistency. Simply stopping at whether trait X or trait Y has phylogenetic signal is of minimal use and, by itself, does not provide enough detail regarding the mechanisms giving rise to the pattern. Thus, measuring phylogenetic signal should not be a goal unto itself; when the level of signal is measured, it should then be utilized and dissected in downstream analyses as necessary, and the evolutionary significance of signal cannot (in most cases) be discerned from a community-level study.

9.2. Phylogenetic Diversity for Setting Priorities and Quick Correlative Exploration

Phylogenetic diversity, or the degree of relatedness between species in an assemblage, was originally measured by ecologists using taxonomic ratios and later using phylogenetic branch lengths. The motivations for measuring phylogenetic diversity range from inferring the mechanisms governing community assembly to attempting to finding the best predictor of ecosystem function to setting conservation priorities. The number of phylogenetic alpha and beta diversity metrics are similarly diverse in the literature, to the point that it is difficult to keep track of them and to understand their relative merit and superiority for a given application (Vellend et al. 2011; Tucker et al. 2017). In chapters 2 and 3, I discuss the use of phylogenetic diversity metrics in detail and their historical development. While the motivations for their use differ, phylogenetic diversity metrics almost universally assume phylogenetic signal in traits or niches and assume a Brownian motion model. I have argued throughout, and will argue here again, that this presents a series of important limitations. These limitations can become so severe that levels of phylogenetic diversity cannot be interpreted with much confidence. So, where do we go from here? When should phylogenetic diversity be measured, and what can we do with the results? I will try to, briefly, answer these questions and provide recommendations in the following paragraphs.

My recommendation is that phylogenetic diversity should be measured and utilized in one of three ways. I present these in order of priority. First, phylogenetic diversity should remain an important tool for those setting conservation priorities. I give this recommendation because determining the mechanism underlying the structure, dynamics, and assembly of the ecosystem being considered are not primary objectives. In addition, phylogenetic diversity provides additional information from which priorities can be set and decisions made. Species richness as a metric provides some valuable information, but conveys little to no information regarding the functioning

and evolutionary histories of the species under consideration. Even in those instances where a phylogenetic diversity metric that is highly correlated with species richness is utilized, additional detail is provided and a sophisticated analyst can partition this information in a way that would be meaningful and useful for a decision-maker. Phylogenetic diversity in such work is also, usually, measured on large spatial and taxonomic scales, such that phylogenetic signal may be more likely, thereby making the metric more likely to provide the desired information.

Second, phylogenetic diversity may be used as an independent variable in analyses to indicate when additional important information has not been measured (Cadotte et al. 2009). For example, the response of a system to disturbance may be modeled with respect to functional diversity and phylogenetic diversity. If the traits measured actually provide little information, while the phylogenetic diversity variable accounts for a large fraction of the variation, then we may infer that there are important traits that have gone unmeasured. However, we will not be able to say those unmeasured traits have phylogenetic signal or antisignal. There is not much more information we can squeeze out of that phylogenetic diversity variable. Rather, it serves as a sign telling the researcher that they have missed an important trait or a series of important traits driving their system. The phylogeny could potentially help point the researcher to a list of putative traits if the researcher is able to identify the lineages that account for the change in diversity that is related to the change in the dependent variable. In some instances, it may be so trivial as not measuring traits related to the nitrogen economy of a plant and finding that adding a legume increases phylogenetic diversity and impacts the dependent variable. In other instances, it may be somewhat less obvious, but with enough biological understanding of a clade and the individual species in a community, the signposts might be clear on where to go next. However, one might argue that if one knows that much about the biology of the species, they probably wouldn't start by looking into phylogenetic diversity and they would likely have a good idea of what aspects of organismal function were important in their system.

Third, phylogenetic diversity measures can be used when absolutely no other information is available beyond a species list. For example, if one is simply quantifying species alpha and beta diversity in or across locations, then also measuring phylogenetic alpha and beta diversity may provide some additional information. Again, one will not know how to interpret the results, but it may serve as a useful signpost. For example, imagine that one is analyzing a system they are completely unfamiliar with (not altogether unusual in present-day ecology) and they find that the environment explains

no variation in species richness. It would not be unreasonable to expect that these statistical findings would not hold when phylogenetic diversity is considered. In the first instance, the analyst may conclude that the environment is unimportant, while in the second instance, the analyst would conclude that it is important, but they don't know why. The extra information gained by the second analyst would ideally promote more detailed investigations via the field or literature. In other words, I am suggesting that phylogenetic diversity may be used in a first pass at the data simply to see what is there or not there. However, this should not be an endpoint of investigation, and downstream analyses should simply use the phylogenetic diversity measure as an indicator that something important (with phylogenetic signal or antisignal) is still not being measured.

9.3. Phylogenies Should Not Be Proxies

The original measurement of phylogenetic diversity using taxonomic ratios had the goal of inferring the mechanisms underlying community assembly. The literature is already heavily trending toward not accepting this inference pathway, due to the uncertainty regarding the degree of phylogenetic signal in traits or niches. This is not even to mention the questions surrounding whether the mechanisms inferred are supported by current theoretical frameworks for species coexistence (Mayfield and Levine 2010; HilleRisLambers et al. 2012). My recommendation for those interested in using the phylogeny as a proxy for similarity in hopes of studying community assembly and dynamics or species coexistence is—don't bother.

The information gained from measuring relatedness alone will not be sufficient to infer mechanisms of community assembly and, worse, may be misleading. The only inference that can be made is whether the community is nonrandomly structured with respect to phylogeny, and that something about relatedness is somehow important. However, even randomly structured communities may arise when phylogenetic relatedness is important. In sum, null results may be truly null or Type II errors, due to opposing mechanisms or lack of phylogenetic resolution (Kress et al. 2009; Swenson 2009a; Swenson and Enquist 2009), and nonrandom results indicate that something about the phylogeny is important. The importance of relatedness will be unknown. We would not know whether it is because closely related species are similar and therefore dominate a community due to superior performance or because they are dissimilar and partition resources. Follow-up studies could be done to disentangle this puzzle, but at that point one is either using a phylogenetic middleman approach (Swenson 2013) or conducting studies that

should have been done in the first place, rendering the original phylogenetic investigation meaningless or a waste of effort. Thus, the optimum we can hope for from such studies is that something might be happening, but we have no idea why and the shortcut we hoped the phylogeny would offer just points us back to the starting line.

The same argument applies with respect to phylogenetic diversity–ecosystem function research. Just as in any other study, the phylogeny will not be a reliable indicator of similarity and, like community assembly research that uses a phylogenetic proxy, it will often be impossible to robustly infer mechanism from phylogenetic diversity. In those cases where the linkage can be made, it will likely be a trivial story where a particular clade represents a new guild or functional group with obvious relevance to ecosystem function. Additionally, these studies do not really tell us that evolutionary history per se impacts ecosystem function more than trait diversity. Rather, both the measured and unmeasured traits have evolutionary histories that vary in their tempo and mode, and the signal of both is captured in the phylogenetic information.

One rationale for the continued use of the phylogeny as a proxy approach is that it is a good overall average measure of similarity. Indeed, as pointed out in recent work, while a single trait may not have signal, multivariate phenotypes will have signal (e.g., Cadotte et al. 2017). This was obvious to Darwin (1859) and to all since. However, ecology is more often not the study of average phenotypes or general phenotypic similarity. Rather, it is more likely a single trait or niche axis that dictates the outcomes of ecological interactions. Thus, even if 99% of the traits have phylogenetic signal, the one trait of importance may not have signal. This may seem like an unrealistic scenario, but if we consider how lineages diverge and the role of ecology in that process, then it becomes clear why it is quite reasonable (Sobel et al. 2010; Swenson 2011a). That is, lineages do not typically diversify into different average phenotypes. Much of the phenotype is retained, and individual trait axes having to do with reproduction and other biotic and abiotic interactions that the lineages are independently experiencing will change more rapidly. While all trait axes will likely be important, if the two lineages co-occur in the future, it is likely the few axes that have diverged that will dictate the strength of their interactions. Thus, the argument that relatedness captures multivariate similarity may be true, particularly on large taxonomic scales, but we have reason to be skeptical that overall similarity is enough to indicate what mechanisms are generating the observed patterns.

One last consideration before I end this section is the interpretation of phylogenetic signal in a trait and the ability of phylogenetic relatedness to

predict an ecological pattern. First, there are clear reasons why phylogenetic distance itself should not be a good linear predictor of ecological similarity even with phylogenetic signal in the trait. Rather, a curvilinear relationship is expected (Letten and Corwell 2015). Distance-based measures do not capture this nuance, and therefore won't be perfect indicators of similarity even in optimal situations. Additionally, the phylogenetic signal in a trait and the ability of phylogeny to predict an ecological pattern does not necessarily indicate that the trait is related to the pattern. Specifically, if two traits evolve under Brownian motion on the same phylogeny, they do not have to be strongly correlated. Thus, linking a phylogenetic diversity result to phylogenetic signal in a given trait is not trivial, and signal in one trait has nothing to do with signal in other traits or the trait diversity that drives interactions. This is likely obvious to most phylogeneticists, comparative methods researchers, and those familiar with Brownian motion, but I am afraid this point is often lost on ecologists. Thus, average phenotypic similarity or the linking of traits with signal to phylogenetic results as rationales for a phylogenetic proxy approach are flawed from my perspective.

In sum, it is very clear why community ecologists have used relatedness as a proxy to represent the average phenotypic similarity of species as a pragmatic first step toward uncovering the drivers of community structure, dynamics, and assembly. However, this average phenotypic similarity is violated in some cases, and there is good reason to believe that individual traits that have diverged at a greater rate than the rest of the phenotype may be those that ultimately determine the interactions between species. Ecology has gotten about as far as it can get with the phylogenetic proxy approach, and it is time to admit the limitations of it and move on. The proxy should be abandoned, and the blind use of relatedness in our analyses should only be used as an indicator that something that has gone unmeasured is of importance, it has phylogenetic signal or antisignal, and that signal has nothing to do with the signal in the traits already measured.

9.4. Phylogenies Should Be Backbones

The recommendation that phylogenies should not be used as proxies for ecological similarity may lead one to think that phylogenetic information has little to no role to play in community ecology. This is not the case. The role of phylogenetic information, though, should be dramatically changed. In chapter 5, I argued that phylogenies be utilized in a backbone or context upon which other information is placed. This is not a new approach, or suggestion, and the most impressive documentations of community assembly have

come with the use of phylogenies as backbones and not as proxies (e.g., Losos et al. 1998; Gillespie 2004). In taking the phylogeny as a backbone approach, several intermediate hurdles will need to be cleared, but they are not insurmountable. Here, I will briefly outline those intermediate steps and why they are important and useful.

The backbone approach can be used to infer the evolutionary history of a variable. This could be the geographic distribution, niche, or trait data associated with the species. To make such inferences reliably, a dense taxonomic sampling of species is needed. For example, if a researcher is focused on a particular family or genus, sampling only those species found in one area may or may not be a very biased sample. If the species in a region are monophyletic, potentially due to a single colonization and followed by diversification within the region, the sampling of the species from this family or genus in just that region is sufficient. This is most likely to be the case in some insular systems. In the vast majority of cases, though, the species being studied are paraphyletic samples, such that many closely and distantly related species are not sampled. This introduces a great deal of uncertainty into the reconstruction of evolutionary history. This will force those that study community assembly to push the spatial extent of their analyses far beyond the local-scale communities they typically study.

A second challenge will be to consider whether studying a single clade is "community ecology." In systems like the Caribbean *Anolis*, the study of a single clade is easily considered community ecology. However, tree communities in these same Caribbean ecosystems can contain tens of families and genera sampled from across the phylogeny of plants. The most diverse tree genus in these systems (e.g., *Miconia* [Melastomataceae] or *Psychotria* [Rubiaceae]) may constitute fewer than 10 species (i.e., ~10% of the tree species) and may be incredibly diverse globally (i.e., ~1,000 species) (Muscarella et al. 2014; Swenson and Umaña 2014). Thus, what can we really learn about the evolutionary history and assembly of species from this genus when roughly only 1% are being studied and they are not monophyletic? Furthermore, what can we learn about the assembly of a tree community when only studying a lineage that represents less than 10% of the species? The challenge, therefore, represented by the backbone approach is not easily surmounted from this perspective. However, a logical starting place is focusing on lineages that dominate the community or communities of interest that also are not terribly diverse globally. Given that locally diverse genera are also often globally diverse (see the *Miconia* example above), locally diverse genera are not always reasonable to study. However, the ratio of local to global diversity may be higher in some genera. For example, the hyper-diverse tree community

of Yasuni, Ecuador, contains over 1,000 species in 25 hectares (Valencia et al. 2004). Within that community are ~40 co-occurring species of the genus *Inga* (Fabaceae). The genus is restricted to the Neotropics and likely contains ~300 species (Pennington 1997). Thus, ~10% of the species known globally occur in one community. That is a tremendous research opportunity for the phylogeny as a backbone approach. Similarly, 10 *Protium* (Burseraceae) co-occur in that community out of the ~140 species known globally (Valencia et al. 2004; Fine et al. 2013). Genera in the Dipterocarpaceae, *Aglaia* (Meliaceae), and *Macaranga* (Euphorbiaceae) represent a similar opportunity in southeast Asian tree communities (e.g., Davies et al. 1998). To some extent, this is already being accomplished in the palm family, Arecaceae, as well (Svenning 2001). Systems such as these represent the logical starting points that should be exploited further with a phylogeny as a backbone approach.

The pursuit of well-sampled phylogenies for ecologically dominant lineages is not sufficient to understand the drivers of community assembly. Samples of communities and their dynamics (i.e., good old-fashioned fieldwork) are needed, as are detailed measurements of those aspects of organismal form and function that dictate ecological outcomes. While these are challenges that ecologists are more familiar with tackling, the seasoned ecologist will also know they are not easy to tackle. For example, there is a large difference between reconstructing species ranges and co-occurrence from global geo-referenced collection data and on-the-ground measurements of fine-scale species distributions and demographic rates that are so vital for truly understanding the drivers of community dynamics. Furthermore, our understanding of the functional ecology of most species in our communities is poor. The phylogeny as a backbone should help in this regard, as it demands a focus on a group of species and a more intimate knowledge of the natural history and functioning of the species under study. Thus, while easily measured functional traits serve as a nice starting point, the phylogeny as a backbone approach should keep digging deeper into the functional ecology. This may be accomplished using functional phylogenomic approaches such as those I discussed in chapter 7 or via other methods. Ultimately, the ecological interactions and traits that govern those interactions are more detailed than what can be gained from easily measured traits, and the phylogeny as a backbone researcher is challenged to measure this detail that functional trait and phylogeny as a proxy researchers often avoid.

The final challenge with the backbone approach is elucidating the feedbacks between local-scale ecological interactions and the processes and patterns at larger scales often studied by phylogeneticists. That is, phylogenetic information can be used to trace how evolutionary history impacts present-

day ecological patterns and interactions, but the study of present-day interactions can inform our understanding of the evolutionary history of a lineage. Thus, the flow of information between the two scales and phylogeny and ecology goes in both directions, with each informing the other and refining their inferences and understanding of the system. Elucidating how ecological interactions and microevolution influence macroevolutionary rates is not a simple challenge, but it is not one that phylogenetic ecologists should lose sight of in their research program.

9.5. Phylogenies Are Best Utilized on Large Scales

The phylogeny as a backbone approach should extend from the study of community ecology to nearly all phylogenetic ecology. These studies will most frequently be conducted on large spatial scales. This is, largely, out of necessity, as dense taxonomic sampling of clades often requires sampling species from across regions. However, this is not the only reason why I urge phylogenetic ecology to move more toward analyses on large spatial scales. I also recommend this scaling out because this is where phylogenetic information is most likely to be valuable for tackling grand challenges in ecology. For example, the latitudinal gradient in species diversity is the focus of intense study, and phylogenetic information has been absent for much of the conversation. When phylogenetic information is included in the conversation, it has often been more of a conceptual discussion, with few detailed analyses. A great example of this is the role of tropical niche conservatism driving the latitudinal gradient (Wiens and Donoghue 2004). Originally, phylogeny was discussed in a conceptual way, which is understandable given the lack of data and the natural progression of an idea. However, the analyses that have followed have been very wanting in detail, and often do not even directly speak to the hypothesis. The distribution of family and genus ages across latitude is a fairly weak test for the niche conservatism hypothesis. More detailed analyses considering the transition between different climates have been accomplished (Zanne et al. 2014; but see Edwards et al. 2015), but even these tests are wanting in detail regarding specific clade histories and divergences, due to sparse trait, spatial, and phylogenetic data sets.

Beyond the niche conservatism hypothesis, we have seen how phylogenetic information is relevant to ecological opportunity and priority effects—topics often discussed by ecologists only on local scales, but also relevant on larger scales (Lee et al. 2012; Leopold et al. 2015; Tanentzap et al. 2015). Additional studies regarding the timing of colonization and how that is, or is not, related to ecological dominance in a region would prove useful particularly

in mainland systems. Similarly, topics like ecological fitting are likely well suited to a large-scale phylogenetic approach. Specifically, ecological fitting is the present-day interaction between two species that did not speciate in the same location (Janzen 1985; Brooks et al. 2006; Agosta and Klemens 2008). Thus, their present-day interaction is due to dispersal into the same location or asymmetrical dispersal into one or the other location and a fitting that may or may not be facilitated via phenotypic plasticity. Janzen originally considered ecological fitting in the context of plants and herbivores, but the concept can be generalized. Indeed, in many instances, we are observing assemblages where the species are a collection of pairs that have long histories of co-occurrence and other pairs with relatively little experience co-occurring. How has this difference in the degree of long-term co-occurrence impacted present-day co-occurrence and interactions (Swenson 2006)? Do recently co-occurring species simply fit together nicely? Do they partition habitats on fine scales like they do regionally, as has been found in the tropical plant genus *Psychotria* (Rubiaceae) (Sedio et al. 2013)? Do they have stronger negative interactions, whereas species that have co-occurred for long periods have done so by differentiating and increasing niche differences? These are all fundamental questions that are not well answered in ecology and require a large-scale phylogenetic approach.

Finally, phylogenetic structure can be exploited in or "built into" large-scale ecology, just as it is often considered in the experimental design in local-scale ecological studies. For example, gradients in diversity occur within genera across latitude and species diversity anomalies occur in genera across longitude. These natural gradients, replicated across clades, provide unique opportunities to compare the functional diversity and mechanisms maintaining species diversity in a phylogenetically controlled manner (e.g., Swenson et al. 2016). To understand the power of this, it is worthwhile to consider an alternative. For example, let us consider a study that wants to address the age-old question of how trait space and packing changes across latitude. Classic work on this topic built off the idea that limiting similarity would increase trait space as species were added to the community, and the spacing between species in trait space would be constant (Ricklefs and O'Rourke 1975; Ricklefs and Travis 1980). Alternative hypotheses include the packing of more species in trait space due to weak interspecific interactions or less intraspecific variation due to increased habitat specialization. Tests of this work across latitude are likely confounded by the fact that clade composition and diversity changes in unison with the gradient in species richness. Ad hoc analyses could be used to partition the variation, thereby loosely dealing with the issue, but they may still be unconvincing. A more structured and cleaner approach to

this classic problem is to study multiple genera that have coincident diversity gradients. Thus, overall clade composition does not change across the gradient, and more detailed phylogenetic analyses can address whether the expansion or packing of trait space is associated with the inclusion or disappearance of subclades within genera that have evolved a particular set of functions or traits. Such a study has not been accomplished, to my knowledge. There are examples where a single group has been investigated across latitude or a diversity anomaly, but detailed phylogenetic analyses of subclades have been absent, despite their clear value.

9.6. Conclusions

In this chapter and throughout the book, I have pointed out strengths and weaknesses of phylogenetic ecology in the past and present. My motivation in doing so has been to provide a brief history of the field for the novice, but also to provide a road map for the novice and experienced phylogenetic ecologist alike. The road map diverges in some places substantially from the current trajectory of phylogenetic ecology, but do not let this discourage you. Rather, the road map leads away from those trajectories that have led to a great deal of stagnation and toward a more interesting integration of phylogenetic information in ecology and an approach that will truly allow us to uncover how evolutionary history influences present-day ecological patterns and interactions. There will be some pains experienced during the proposed remodel of phylogenetic ecology, and the temptation of using a phylogenetic proxy and the overinterpretation of phylogenetic diversity patterns will remain, but I think phylogenetic ecology will be much more interesting, substantial, and impactful if we attempt a remodel over the current trajectory.

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