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perspective

Why biogeography matters: historical biogeography vs. phylogeography and community phylogenetics for inferring ecological and evolutionary processes

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Abstract. Phylogenetic and phylogeographic approaches have become widespread in evolutionary biology, ecology, and biogeography. However, analyses that incorporate inferences from historical biogeography (e.g., timing of colonization of a region) may be essential to answer the most important large-scale questions in these fields, but they remain infrequently used. I focus on two examples here. First, I argue that understanding the origins of biodiversity hotspots (and other high-diversity regions) requires comparing the timing of biogeographic colonization and diversification rates among regions. In contrast, phylogeographic studies (e.g., analyses within species within a region) may themselves say little about why a region is diverse relative to others. Second, incorporating historical biogeography can help address the processes that determine community species richness and structure, such as dispersal, in-situ trait evolution, and in-situ speciation. In contrast, the widespread “community phylogenetics” approach (focusing on relatedness of species in communities) may have limited ability to explain community richness and structure.

Keywords. biodiversity hotspot, biogeography, community ecology, community phylogenetics, phylogeny, phylogeography, species richness

In the fields of ecology and evolutionary biology, many of the patterns that we are most interested in involve multiple species. For example, why do some regions have more species than others? What explains the number of species in a community and the ecological traits that they possess? What explains the diversity of phenotypes in a clade? Despite the importance of these questions, it is generally difficult to address them with an exclusively experimental approach, since many of these patterns arise over time scales at least as long as those needed for new species to arise (i.e., millions of years).

The fields of biogeography and phylogenetic biology both offer many approaches to help address the origins of these larger-scale patterns. For example, many questions about biodiversity are now addressed through biogeographic comparisons of different regions (e.g., global patterns of species richness; Buckley and Jetz 2007). Similarly, it has now become routine to study patterns of trait evolution using phylogenies. Many studies now address questions about community ecology

by analyzing patterns of phylogenetic relatedness among the species present in one or more communities (e.g., Webb et al. 2002, Cavender-Bares et al. 2009).

Nevertheless, many of the most interesting questions in ecology and evolution may benefit from a combination of phylogeny and biogeography, and this is not routinely done. Specifically, addressing these questions should include inferences about the pattern and timing of biogeographic dispersal between regions. Such inferences, based on analyzing biogeographic patterns in the context of a time-calibrated phylogeny, are part of the modern field of integrative historical biogeography (e.g., Donoghue and Moore 2003, Wiens and Donoghue 2004, Lomolino et al. 2006). Here, I will focus on two related topics in ecology and evolution that would benefit from the input of historical biogeography: the origins of biodiversity hotspots and the assembly of ecological communities. I will contrast approaches that incorporate historical biogeography with alternative approaches that are often used to answer them in-

stead, specifically, phylogeographic analyses and community phylogenetics. In both cases, incorporating historical biogeography can expand the scale and scope of the studies used to address these topics (both geographically and temporally), and offer a more complete picture of the relevant evolutionary and ecological processes.

Origins of biodiversity hotspots and other species-rich regions

A fundamental question in the fields of ecology, evolution, and biogeography is why some regions have more species than others. Many phylogeographic studies are conducted with the stated goal of understanding the origins of biodiversity hotspots and other high-richness regions (e.g., California: Calsbeek et al. 2003; Amazonia: Funk et al. 2007; southeast Asia: Morgan et al. 2011). Phylogeography addresses spatial patterns of genetic differentiation within species and/or among species that are very closely related (e.g., Avise 2000, Hickerson et al. 2010). Phylogeographic studies are critically important for conservation (and many other areas as well). For example, they often reveal the presence of cryptic lineages that are not apparent from morphological variation alone (e.g., Bickford et al. 2007). But they may tell us little about the origin of biodiversity hotspots and other species-rich regions.

To understand why not (and why historical biogeography matters), we need to think about how species richness patterns arise. Species richness patterns ultimately arises through the processes of speciation, extinction, and dispersal (Ricklefs 1987), and any complete explanation for richness patterns must ultimately relate to these processes (although many ecological and evolutionary factors act on these three processes to drive richness patterns). Given the primacy of these three processes, patterns of high richness in a particular region for a particular group of organisms are likely to be explained by one (or both) of two patterns (Wiens 2011): either greater time in a region (i.e., earlier colonization, leaving more time for speciation to build up richness relative to other regions; Stephens and Wiens 2003) or higher net diversification rates (where diversification rates

represent the balance of speciation and extinction over time; review in Ricklefs 2007). These contrasting explanations are illustrated in Figure 1.

To understand higher diversity in a region for a particular group of organisms we need to use historical biogeography to infer the timing and patterns of colonization, given that a region may be more diverse simply because it has been inhabited longer (e.g., Stephens and Wiens 2003). We can also use phylogenetic approaches to infer rates of diversification in those regions as well and test whether diversification rates are higher in clades inhabiting more diverse regions (e.g., Ricklefs 2007). Diversification rates may be higher in a given region because ecological conditions there either promote speciation, buffer lineages against extinction, or some combination of these processes. Importantly, there must be a comparison of the timing of biogeographic colonization and of diversification rates and patterns between regions in order to understand why some regions have more species than others. Thus, historical biogeography is essential.

Given this perspective, phylogeographic studies of species within high-diversity regions have three critical limitations for understanding the diversity of these regions. First, we would like to know: what makes these biodiversity hotspots and other high-richness regions special? Fundamentally, answering this question must involve a comparison between regions. Therefore, one cannot answer this question simply by analyzing phylogeographic patterns within one such region. However, such single-region studies are the norm, and “comparative phylogeography” generally refers to comparisons of different lineages in the same region, not patterns in different regions.

Second, because phylogeographic studies focus on within-species patterns, they are (almost by definition) limited to relatively recent time scales (i.e., the age of the most recently diverged species). Although some genetic diversity and species diversity may be generated at this shallow time scale, it may not be the time scale at which major differences in species richness between regions are generated. For example, in hylid tree-frogs, diversity differences between Amazonia and

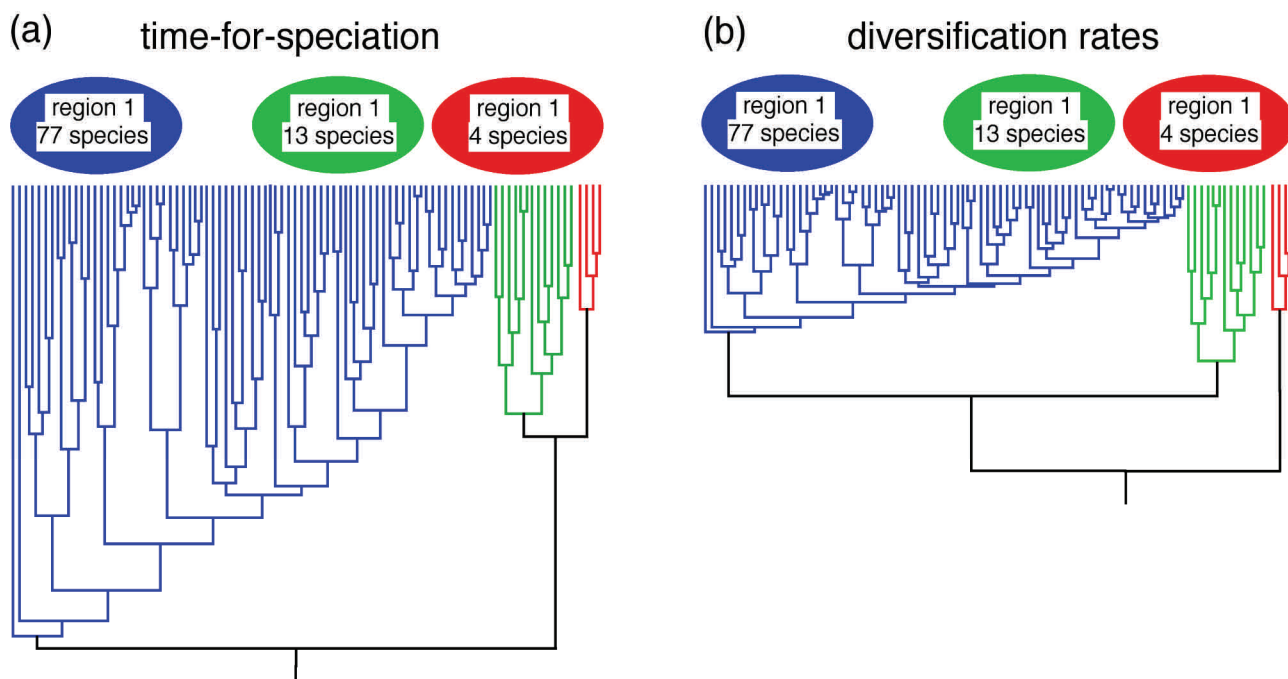


Figure 1. Two general explanations for differences in species richness among three hypothetical regions, illustrated on two time-calibrated phylogenies (with branch lengths proportional to time). In (a), the higher richness of region 1 is explained by historical biogeography: there are more species in this region because it has been inhabited by this clade longer than the other regions have been, and there has been less time for speciation to build up richness in regions 2 and 3 (time-for-speciation effect: e.g., Stephens and Wiens 2003). In (b), analyses of historical biogeography show that region 1 was colonized relatively recently, and the higher richness is explained by higher rates of net diversification in this region (caused by a higher net rate of speciation, a lower net rate of extinction, or a combination of these factors).

other regions began to develop more than 75 million years ago (Wiens et al. 2011). In fact, if all the diversity in a region for a given clade was generated at the temporal scale of phylogeographic studies, the region should have only a handful of species! The contrast between the temporal scope of phylogeography and historical biogeography is illustrated in Figure 2.

The third issue relates to limitations on inferences about speciation from phylogeographic studies. On the positive side, phylogeographic studies may provide important insights into speciation (e.g., Calsbeek et al. 2003, Funk et al. 2007). But such studies may be relevant to explaining high species richness of regions primarily under two conditions: (a) when differences in speciation rates potentially explain differences in diversity between regions, as suggested by large-scale comparisons of diversification or speciation rates in different regions, and (b) when there is a comparison of patterns of speciation between regions, which will help reveal why speciation rates differ between them. Again, an analysis of one region

alone will not tell us why regions are different.

An additional, related limitation in phylogeographic studies of speciation is the implicit assumption of uniformity. Unless all the diversity of a region was generated with the most recent speciation events (which seems unlikely), then the relevance of phylogeographic studies of speciation will depend on projecting the processes that are revealed backwards much further in time. In other words, one has to assume that the processes generating species in the last few million years or so are the same processes that generated them in the more distant past, and that any differences found between regions have been largely consistent over the relevant time scales for generating the observed diversity differences. This uniformity may be a valid assumption in some cases (e.g., comparing phylogeography of marine vs. terrestrial organisms), but more questionable in others (e.g., comparing regions that are influenced by Pleistocene glaciations to those that are not).

Origins of community diversity and structure

I now shift from the diversity of species in regions to the diversity of species and phenotypes at local sites within a region. In the past 10 years, there has been an exciting increase in the application of phylogenies to community ecology (recent reviews in Cavender-Bares et al. 2009, Vamosi et al. 2009). However, many of these studies do not consider historical biogeography. What can we learn about community ecology from incorporating historical biogeography that we cannot learn from phylogeny alone?

To answer this question, we first need to consider what it is that we want to know. Much of the recent literature on phylogenetics and community ecology has focused on a very specific question: whether communities are more strongly influenced by competition or environmental filtering (e.g., Cavender-Bares et al. 2009). Simply put, when species in the community are more closely related than expected by chance (relative to a random sample of species within the region), this pat-

tern is often taken to indicate environmental filtering (if close relatives share similar environmental tolerances). On the other hand, if species are more distantly related than expected by chance, this pattern is often assumed to represent the effects of competition (if close relatives share similar traits and resource requirements and therefore cannot co-exist). In both cases, the interpretation hinges on relevant ecological traits being evolutionarily conserved among species.

I use the term “community phylogenetics” to refer to this general approach that is based primarily on the relatedness of species in one or more communities, and distinguish this approach from the more general application of phylogenies to questions in community ecology. In recent years, the field of community phylogenetics has exploded in popularity (Cavender-Bares et al. 2009, Vamosi et al. 2009). Indeed, many studies now focus primarily on explaining patterns of phylogenetic structure in communities, rather than focusing on more conventional attributes of com-

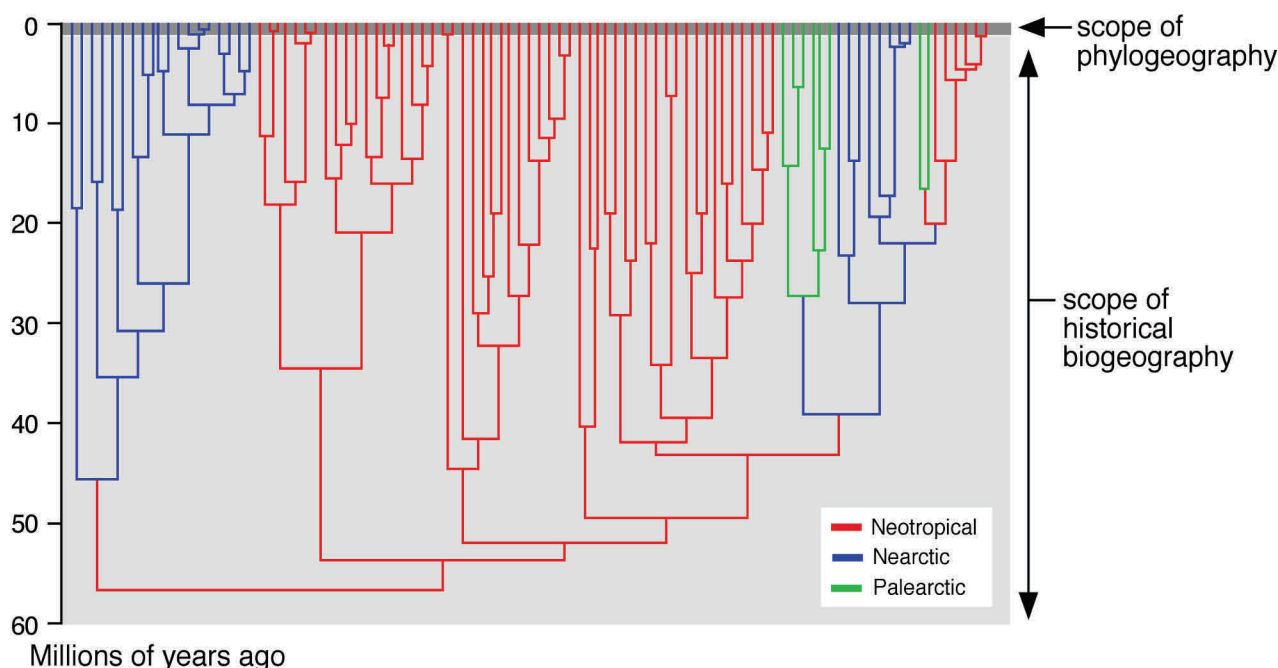


Figure 2. An illustration of the differences in the temporal scope of phylogeography versus historical biogeography for explaining differences in diversity between regions. By definition, phylogeography is restricted to the most recent temporal scope (i.e., patterns of genetic diversity within species and/or among very closely related species) and rarely involves comparison between regions. In contrast, historical biogeography involves comparisons between regions at deeper temporal scales. These deeper temporal scales may be more relevant for explaining differences in diversity between regions. This illustration is based on a time-calibrated phylogeny and geographic data from tree-frogs (tribe Hylini; from Wiens et al. 2011). Note that the exact temporal scale of phylogeography can be group specific (i.e., within-species patterns may be older or younger, depending on the group).

munities, like species traits or species richness.

Yet, there is another set of questions that we might ask about communities from a phylogenetic perspective, and these questions may be best addressed by incorporating historical biogeography, along with information on phylogeny, local communities, and species traits. First, it is important to remember that only a limited number of processes can directly determine the richness of a local community and the ecological traits present among the species in it. These processes (Figure 3) are: dispersal of species into that community, extinction of species in the community, in-situ speciation in that community (or at least “in-situ” relative to other communities being com-

pared), and in-situ trait evolution (e.g., Losos 1996, Stephens and Wiens 2004). Many other processes will then act on these four processes to create patterns of community diversity and structure (such as competition, disturbance, facilitation, and environmental limits on dispersal). Interestingly, none of these four processes are directly addressed using a traditional community phylogenetics approach (although, to be fair, environmental filtering may reflect the outcome of local extinction or ecological constraints on dispersal; e.g., Cavender-Bares et al. 2009). In contrast, a phylogenetic approach incorporating historical biogeography can help identify dispersal events and distinguish dispersal-driven community

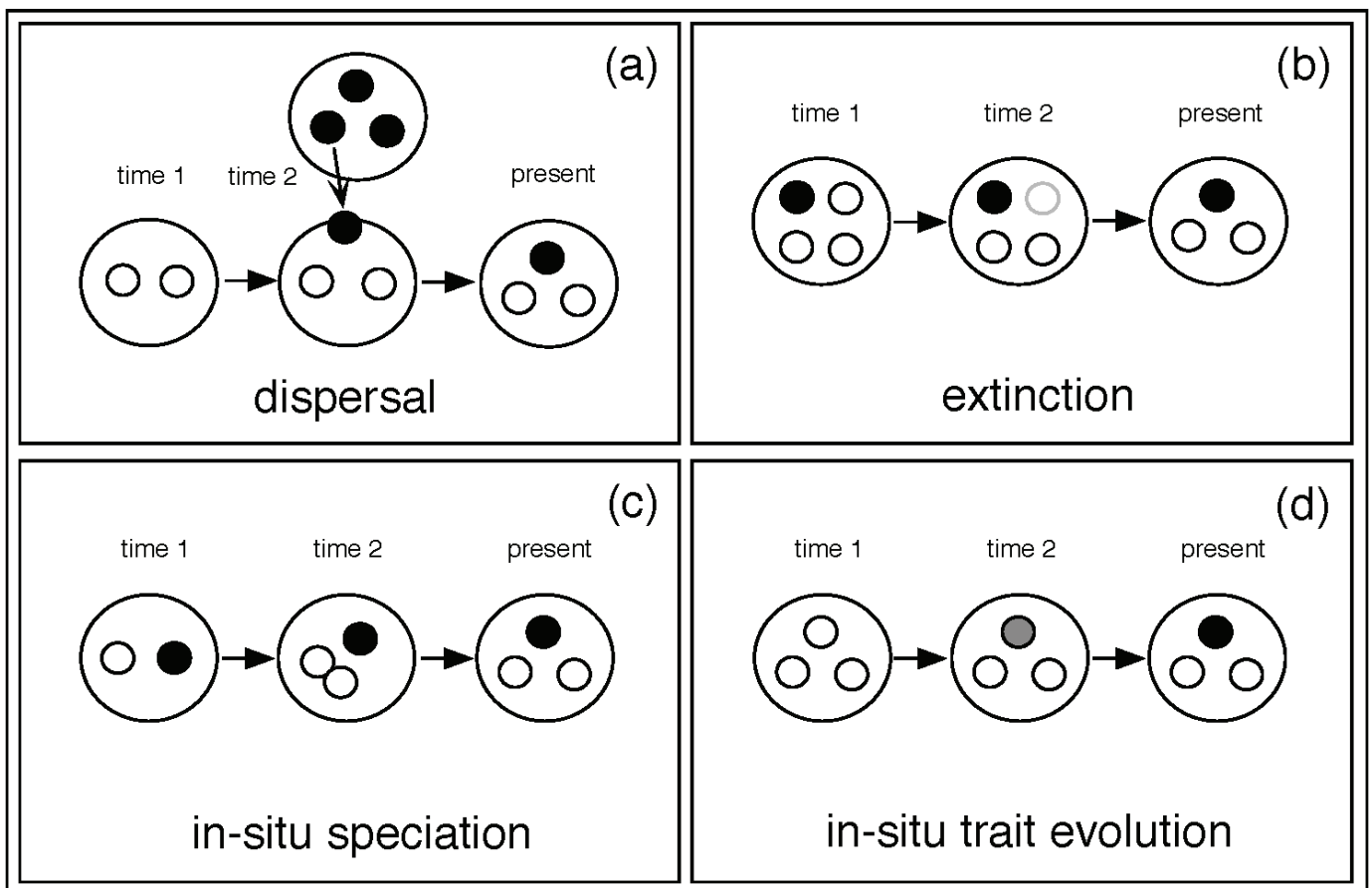


Figure 3. An illustration of the four general processes that determine community diversity and structure (i.e., the number of species in a community and their traits). In the present-day community (large circle on far right in a–d), there are three species, two with state A for a given ecological character (the two small unfilled circles) and one with state B (the small filled circle). In (a), there is initially two species with state A (time 1), and then a species with state B is added through a dispersal event (time 2) from a nearby community where all species have state B (above, with three filled circles). In (b), there are initially four species, three with state A and one with state B (time 1). The present-day community composition arises through the local extinction of a species with state A (time 2). In (c), there is initially one species with state A and another with state B (time 1), and a second species with state A is added by in-situ speciation of the original species with state A (time 2). This could occur through sympatric speciation, or through allopatric or parapatric speciation (depending on the scale of the local community). In (d), there are initially three species with state A (time 1), and state B is added by in-situ evolution within one of these species (time 2).

changes from those due to in-situ speciation and in-situ trait evolution (in other words, it can help address three of the four processes).

Given this perspective, some of the questions of interest include: why do some communities have more species than others? What explains the diversity of ecological traits among the species in a community? Did these traits evolve in the community due to interactions with the existing set of species? Or did a given trait evolve in a different region and become added to the community through dispersal? Conversely, do biogeographic barriers (e.g., different habitat types or climate) lead to differences in community structure between communities within a region? Can species with a given trait be added to a community in which species with that trait are already present? How does the presence of species in a community or region (and their traits) influence the evolution of lineages that have subsequently dispersed into the region or community? For example, do these pre-existing species influence the patterns of diversification of lineages that arrive later (i.e., in-situ speciation)? Do they influence their patterns of in-situ trait evolution?

A very limited number of studies are starting to address these questions by incorporating historical biogeography into phylogenetic studies of community ecology (full disclosure: the examples below are from my lab). For example, in treefrogs, patterns of timing of biogeographic colonization of different regions seem to strongly influence the richness of local communities within each region (i.e., communities in regions colonized earlier have more species), and seem to explain the high local diversity in the Amazon Basin relative to other regions (e.g., Wiens et al. 2011). Similarly, the timing of colonization of different habitats (i.e., climatic zones) within regions seems to explain differences in local diversity between habitats within regions in salamanders (Kozak and Wiens 2012). Analyses of Middle American treefrogs (Moen et al. 2009) suggest that community structure in lowland habitats is strongly influenced by dispersal of lineages into Middle America that retain their ancestral ecological traits as they disperse (ecologically conservative dispersal, ECD;

Stephens and Wiens 2004), whereas montane communities are more strongly influenced by in-situ trait evolution. Surprisingly, the results also show that many communities have ecologically similar, co-occurring species in which one or more species have been recently added through ECD (suggesting that their similarity to species already there does not prevent their dispersal into communities). In contrast, limited ECD seems to explain differences in community structure (in terms of microhabitat specialists) in emydid turtles in eastern North America (Stephens and Wiens 2004). These are just a few examples of patterns that have been found by incorporating historical biogeography into analyses of community ecology.

Of course, analyses of community ecology that incorporate historical biogeography can also have many limitations. One important limitation is that historical biogeography is typically carried out at the scale of regions. In contrast, community structure may instead be determined largely by processes occurring at finer scales within regions. However, this remains an open question, and one that may be better answered by incorporating historical biogeography, rather than simply ignoring it. This may also depend on which communities within the region are considered (Moen et al. 2009). In addition, many of the same basic ideas from historical biogeography may apply within a region. For example, different habitats within a region may act like different regions, and similar processes and methods may apply (e.g., differences in local richness across habitats in salamanders are seemingly determined by the timing of colonization of different habitats; Kozak and Wiens 2012). Another major concern is that biogeographic reconstructions are not accurate. However, using likelihood methods (e.g., Ree and Smith 2008), it is possible to evaluate when biogeographic reconstructions are statistically well-supported, and when they are not. Thus, one can detect when inferences should be reliable (although more study of these confidence measures would be desirable). Given this, simply assuming that all biogeographic reconstructions are uniformly untrustworthy seems to be based more

on faith and belief, rather than scientific evidence. It should also be noted that neither biogeographic nor community phylogenetics approaches presently have methods to estimate or otherwise address the impacts of local extinction of species on community structure and richness, even though local extinction may be a critically important driver of community patterns (Morin 1999). Also, methods for inferring community-related processes from historical biogeography are not as well developed and tested as those for community phylogenetics (e.g., Kraft et al. 2007). But similar methods can be developed and tested to address these questions, and some progress has been made in this direction (e.g., Moen et al. 2009). Finally, and perhaps most importantly, neither of these phylogenetic approaches to community ecology should be a replacement for more traditional observational, experimental, and theoretical approaches to the field, but instead are just parts of a broad set of tools for addressing questions about ecological communities.

Conclusions

Multiple approaches will be required to resolve many of the most exciting and challenging large-scale questions in ecology, evolutionary biology, and biogeography. Historical biogeography, especially the inference of when lineages colonized a region, should be an essential tool for many of these questions. Here, I have argued that incorporating historical biogeography may be particularly useful for understanding the origins of biodiversity hotspots and patterns of community structure and richness. However, these are just two examples, and historical biogeography may be relevant to many other areas as well (e.g., trait evolution). Finally, I note that the goal of this piece is not to discourage researchers from doing phylogeography or community phylogenetics, but simply to encourage researchers to also consider the broader-scale insights that can come from incorporating historical biogeography as well.

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