



Historical biogeography, ecology and species richness

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Ecology and historical (phylogeny-based) biogeography have much to offer one another, but exchanges between these fields have been limited. Historical biogeography has become narrowly focused on using phylogenies to discover the history of geological connections among regions. Conversely, ecologists often ignore historical biogeography, even when its input can be crucial. Both historical biogeographers and ecologists have more-or-less abandoned attempts to understand the processes that determine the large-scale distribution of clades. Here, we describe the chasm that has developed between ecology and historical biogeography, some of the important questions that have fallen into it and how it might be bridged. To illustrate the benefits of an integrated approach, we expand on a model that can help explain the latitudinal gradient of species richness.

Biogeography is closely tied to both ecology and phylogenetic biology [1]. For example, the theory of island biogeography [2] is widely considered to be fundamental in ecology. Similarly, biogeography is a major topic in classic texts on phylogenetic systematics [3,4]. Given these long-standing connections, an outsider to ecology and evolutionary biology might assume that biogeography is an integrative discipline that combines phylogeny and ecology to address important questions about the distribution of lineages and global patterns of diversity. Unfortunately, that assumption would generally be incorrect.

Currently, biogeography is far from being the meeting place of ecology and phylogenetics. Instead, much of phylogeny-based (historical) biogeography ignores ecology, both in terms of the questions that it asks and the answers that it provides. Similarly, ecologists do not generally incorporate historical biogeography, even when it is crucial for addressing some of their central questions. Here, we describe our view of the problematic state of contemporary biogeography and the potential benefits of a more integrated field. As an example, we focus on a major problem in ecology and biogeography, the latitudinal gradient in species richness.

The current separation of historical biogeography and ecology

Although ecology, phylogeny and biogeography were once blended rather seamlessly by naturalists and pre-cladistic taxonomists, a major chasm now separates these research areas. For the past three decades, historical (phylogenetic) biogeography has been concerned primarily with deriving cladograms for areas based on the phylogenies of the organisms inhabiting these areas [5–10]. Although useful tools have been developed, some important components have been ignored. One of these is time, which has been addressed elsewhere [11]. The other is ecology (Box 1).

But what is the biological significance of finding a particular set of area relationships (i.e. a history of geological connections among regions, or an area tree)? Some authors have discussed the use of area cladograms in answering evolutionary and ecological questions; for example, in distinguishing modes of speciation [12,13] and reconstructing patterns of community assembly [6]. However, these discussions have remained mostly hypothetical and more attention has been given to how to estimate area trees rather than to actually using them [5,7–10]. More importantly, by focusing almost exclusively on area cladograms, historical biogeography has divorced itself from biological questions that it might be uniquely qualified to help answer.

Similarly, many taxon-oriented phylogenetic studies address the biogeographical implications of their results [14,15]. These studies typically relate their findings to hypotheses of geological connections among areas, sometimes using a molecular timescale to associate geological and phylogenetic events. Some of these studies have mentioned the influence of ecology on such patterns (e.g. intermittent dispersal of warm-climate adapted lineages between temperate forest regions [16]). However, they generally do not set out to address the ecological processes that explain large-scale biogeographical patterns.

On the ecological side, ecologists typically do not consider historical biogeography (with some important exceptions [17–19]). There has already been much discussion about the importance of phylogenies to ecology (e.g. using phylogenies to study the evolution of ecological traits and the relationships among species in a community; [6,19]). However, we think that the importance of phylogenetically informed biogeography goes beyond the traditional uses of phylogenies in ecology. Specifically,

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Box 1. Ecology and area cladograms

Ecology can be crucially important to historical biogeography, even if one's goal is only to reconstruct relationships among areas of endemism (i.e. cladistic biogeography). For example, area cladograms do not depend solely on the history of geological connections among areas, but instead on the history of connections among suitable habitats. It is easy to imagine cases where the history of connections among habitats in different areas differs from the history of geological connections (e.g. even though Mexico has always been geologically connected to North America, many of the lowland taxa in Mexico originated in South America, whereas many highland taxa originated in North America [1]).

Cladistic biogeography has considered primarily three processes in explaining biogeographical patterns: (i) vicariance; (ii) dispersal; and (iii) extinction [5–10]. Generally, vicariance is assumed to be the main cause of concordant phylogenetic patterns among co-distributed clades, and dispersal and extinction are invoked primarily to explain discordance among clades. However, dispersal, vicariance and extinction are all linked directly to ecological processes, and the likelihood that any of these processes explains a given pattern depends on ecological factors, such as dispersal ability and habitat fidelity. Little attempt has been made to bring ecological information to bear on cladistic biogeography.

New GIS-based methods for ecological niche modeling offer one approach for incorporating ecological information in cladistic biogeography. Given data describing the climatic conditions for locations where a species or clade exists today, an ecological niche model can be made to predict where a species or clade occurs, given its inferred environmental tolerances [44]. Assuming that these tolerances remain similar over time, and given some information about past climates in the biogeographical region in question, the distribution of acceptable habitats for the lineage can be projected back onto maps for different points in time [45]. Thus, it should be possible to predict pathways for dispersal between areas that are no longer connected by suitable habitat, and reveal areas that lacked sufficient suitable habitat at crucial points in the past (suggesting local extinction). Such analyses might also illuminate the relative timing of biogeographical connections and barriers.

We think that even crude ecological information (e.g. about general climatic tolerances of taxa and past climates of regions) can offer invaluable insights into cladistic biogeography. For example, dispersal of some terrestrial groups between continents not only requires a terrestrial connection, but also suitable climate in the region of that connection during the time frame of the putative dispersal event [46].

historical biogeography can contribute to two main areas of ecology.

The first is the study of large-scale patterns of species richness. Beginning during the 1960s, the problem of explaining patterns of species richness became an issue in ecology rather than in historical biogeography [17]. This appears to have occurred through both a conceptual expansion of ecology and a conceptual contraction of historical biogeography during the 1970s and 1980s with the advent of cladistics [3,4]. But questions about large-scale patterns of diversity are fundamentally about historical biogeography. For example, increases in species richness within a region can come about only through dispersal of species into a region and/or *in situ* speciation, processes that are best identified using historical biogeography. To understand global patterns of diversity fully, we need to understand how ecology influences large-scale biogeographical patterns within and among clades.

Second, in community ecology, the composition of local-scale communities depends upon the regional species pool [20], and the composition of the regional species pool is, in turn, determined by large-scale biogeographical processes [18–19,21]. Thus, the absence of a given ecological guild from a local community might not be explained by simply examining the ecology or even the phylogeny of the species in that community. Instead, it might reflect the large-scale biogeographical patterns of the group(s) containing the absent guild [22,23].

Of course, it would be unfair to say that large-scale biogeographical patterns have been entirely ignored in ecology [19]. Unfortunately, however, many ecologists seem to view these patterns merely as historical accidents, which are then contrasted with deterministic local-scale ecological processes. This view implies that there are no general principles that determine large-scale biogeographical patterns. However, large-scale biogeographical events are also the outcome of ecological processes, and a dichotomy between historical and ecological explanations is artificial. The problem is that understanding the

processes that cause large-scale biogeographical patterns has not been a major focus of ecology or even, ironically, of historical biogeography. A potentially important area of research appears to have fallen into the chasm that has developed between these fields.

It is tempting to imagine that the field of macroecology [24,25] has addressed the ecological processes that determine large-scale patterns of clade distribution. Unfortunately, macroecology has also tended to neglect such issues and, generally, has not dealt with the biogeography of clades *per se*. Similarly, Hubbell's neutral theory of biodiversity and biogeography [26] addresses patterns of species richness in terms of speciation and dispersal (certainly a welcome approach), but does not directly address the processes that cause large-scale patterns in the distribution of clades. Thus, a question such as 'why do palm trees occur outside of Miami and Bangkok but not New York or Moscow?' is not really addressed in the present disciplines of historical biogeography or macroecology, neither is it a focus of Hubbell's theory. But it is these large-scale patterns of presence and absence of clades between regions that underlie geographical patterns of species richness and community structure.

Integrative historical biogeography

What determines the large-scale distribution of organisms? At the smallest spatial scales, few would disagree that the distribution of organisms within a region is determined by their ecology (or ecophysiology). But larger scale patterns are the outcome of processes occurring at smaller spatial scales, so large-scale patterns must also connect to ecology. What are the specific ecological processes that determine large-scale patterns of historical biogeography? We briefly outline several that might be most relevant.

In general, biogeographical patterns result from ecological processes that influence dispersal (or 'dispersion') at different spatial and temporal scales. For example,

vicariance is usually depicted as an alternative to dispersal, but vicariance is the outcome of processes that restrict the dispersal of individuals within the range of ancestral species [27]. In other words, to understand vicariance requires an understanding of dispersal. Similarly, to understand large-scale patterns of clade distribution, we need to understand why members of a clade have dispersed to some places and not to others.

We consider the following processes to be crucial. Phylogenetic niche conservatism (Box 2) determines which environmental conditions the members of a clade can tolerate, which regions they can disperse into and the nature of the ecological barriers to their dispersal. Conversely, niche evolution (Box 2) enables a given species and its descendants to disperse into new habitats and climatic regimes, and to persist in changing environments. Extinction (whether local, species-wide, or clade-wide) and emigration can also be important explanations for the absence of a clade from a given area. Although extinction need not directly involve dispersal, the absence of a clade from a region owing to extinction or emigration begs the question of why the area has not been recolonized, which again invokes a limitation on dispersal.

Dispersal ability or vagility (e.g. flying versus crawling) determines how rapidly organisms will move within their set of acceptable environmental conditions. Finally, competition with other species can explain the absence of a given species or clade from regions that are within their set of tolerable environmental conditions.

Large-scale geological events, such as continental drift, mountain building and changes in sea level, can obviously have a strong influence on the geographical distributions of clades. But their effects are also mediated through ecological limitations on dispersal, even if some of the most extreme ecological limitations might seem trivial (e.g. sharks are unable to walk on land; maple trees are unable to grow in the ocean).

In summary, the geographical distribution of a given clade will be determined by (i) the ancestral ecological niche of the clade; (ii) the geographical starting point for dispersal; (iii) limitations to this dispersal imposed by abiotic conditions and other species (e.g. niche conservatism and competition); (iv) opportunities for niche evolution that are afforded to individual species by their geographical location (i.e. species are unlikely to adapt to ecological conditions that they are never exposed to);

Box 2. Phylogenetic niche conservatism and niche evolution

Phylogenetic niche conservatism [27,44,47,48] can be a crucial factor in explaining large-scale patterns of distribution. The fundamental niche of a species describes the abiotic conditions in which it can persist and maintain viable populations [49]. We specifically refer to the geographical range, rather than other aspects of the niche (e.g. diet). Although organisms collectively occupy a wide range of environmental conditions on Earth, most species and clades occupy only a limited subset of these. This set of acceptable conditions can be determined by intrinsic organismal traits, such as physiology, and can be maintained over long evolutionary timescales. For example, many groups of organisms are globally widespread in tropical regions, but have not successfully invaded or radiated in temperate regions, despite tens or hundreds of millions of years of opportunity (e.g. onychophorans, cycads and caecilians). If there is niche conservatism within a clade, then the ancestral niche can determine the regions and habitats to which the clade can spread, and those in which it will persist in the face of environmental change. Although niche conservatism can be seen as a pattern or outcome rather than a process, it can be actively maintained by microevolutionary forces over time [27].

Niche evolution (i.e. the expansion of niche breadth or specialization for new conditions) should enable invasion of new habitats and climatic regimes that had previously limited the distribution of a clade (Figure 1). Even though certain niche characteristics might be shared by all members of a clade through phylogenetic descent, niche evolution can only occur in individual species. Thus, changes in niche breadth in one species in one part of the range of a clade might have only a limited impact on the overall distribution of the clade. We think that the interplay between niche conservatism and niche evolution will prove to be a major theme in the biogeographical history of many clades.

Evidence for niche conservatism can come from the repeated failure of a clade to invade habitats or climatic regimes that are adjacent to its geographical range at several independent points (Figure 1), with each point potentially representing an independent replicate for statistical analysis. New GIS-based tools should also facilitate quantification and phylogenetic analysis of niche conservatism and niche evolution [44–45,50]. The strongest evidence for niche conservatism should come from dissecting the ecophysiological traits that underlie the geographical range limits of species and clades, and from determining the microevolutionary forces that limit evolution in those traits.

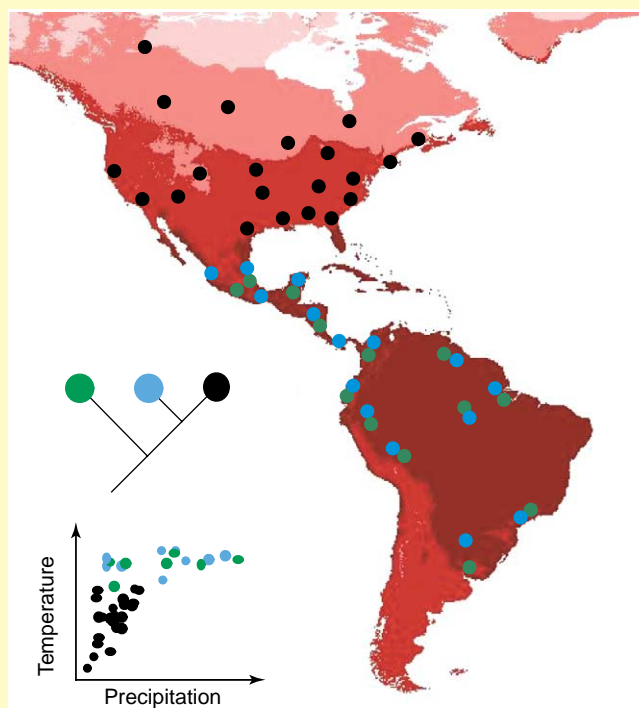


Figure 1. Hypothetical example illustrating niche conservatism and niche evolution. Different colored dots on the map and graph indicate localities for members of three clades. Lighter shades of red indicate colder yearly minimum temperatures. Two of the clades (blue and green) exhibit niche conservatism. Species in these clades are confined to tropical climates and fail to invade cooler regions in North America, southern South America, and high elevations, despite their geographical proximity to these areas (we assume that their spread into these regions is not limited by competition). The third clade (black dots) exhibits niche evolution relative to the other two. This clade has invaded temperate regions (presumably by evolving tolerance to freezing winter temperatures) and no longer occurs in the ancestral tropical climatic regime.

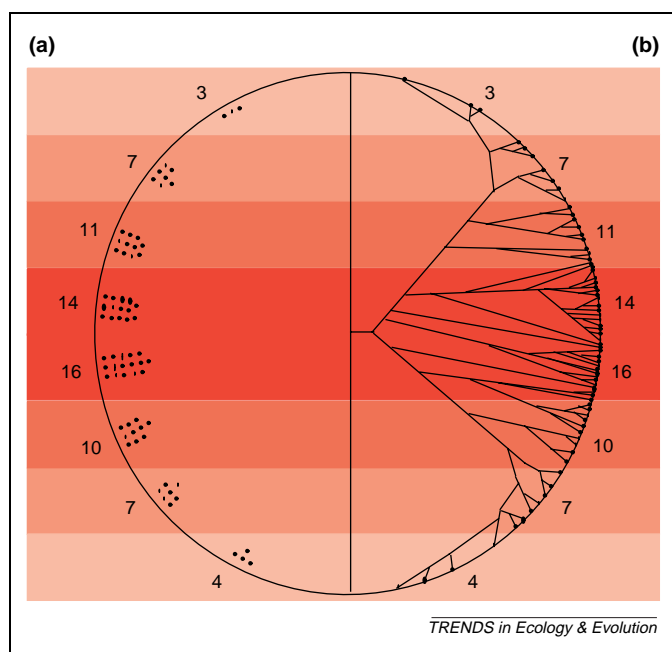


Figure 1. Two approaches to the problem of explaining global patterns of species richness. Standard ecological approaches (a) seek correlations between the numbers of species of a given group at a given location (numbers along the edge of the globe) and environmental variables (e.g. temperature, indicated here by different shades of red). By contrast (b), we advocate considering the biogeographical history of the species and clades that makes up these differences in species richness between regions, and understanding how ecology, phylogeny and microevolution (e.g. adaptation) have combined to shape that biogeographical history. Each dot represents a species and its generalized geographical placement on the globe, and the lines connecting them represent both their evolutionary relationships and the simplified paths of dispersal. (b) also illustrates the tropical conservatism hypothesis, which suggests that there are more species in tropical regions because most groups originated in the tropics and are specialized for a tropical climatic regime, that most species and clades have been unable to disperse out of the tropics (because of niche conservatism), and that the greater time and area available for speciation in the tropics has led to higher species richness in the tropics for most taxa. As shown here, the tropical conservatism hypothesis predicts that temperate lineages are often recently derived from clades in tropical regions, leading to (on average) shallower phylogenetic divergences among temperate lineages than among tropical lineages. Although not illustrated here, an important part of the tropical conservatism hypothesis is the idea that tropical regions were more extensive until the mid-Tertiary, which might help explain the greater number of extant clades originating in these areas.

and (v) the amount of time since the origin of the clade, during which niche evolution and dispersal could occur. The challenge for integrative historical biogeography will be to disentangle and quantify the relative importance of these factors in determining the large-scale distribution of clades.

Integrative historical biogeography and the latitudinal gradient in species richness

The benefits of integrating historical biogeography and ecology can be illustrated by the study of large-scale patterns of species richness. The typical ecological approach focuses on correlations between local or regional-scale richness for a given group or groups of organisms and environmental conditions across several locations (see [28–30] for recent examples and reviews). But correlation is not causation and environmental variables cannot by themselves increase or decrease local or regional species richness: dispersal, speciation and extinction can. The standard ecological approach attempts to answer the ‘why’ of species richness patterns

by looking at ‘how many’ species occur under present-day ecological conditions (Figure 1). The historical biogeography that we envisage determines ‘who did what, where and when’ for each of the individual species and clades that make up the ‘how many,’ and uses all of this information to help answer ‘why’ (Figure 1). This is not to say that ecology and climate are at all unimportant, only that they must act on evolutionary and biogeographical processes (e.g. speciation, dispersal and extinction) to determine patterns of species richness.

An integrative theory for biodiversity patterns

The basic elements of a plausible theory to explain large-scale patterns of species richness in terms of ecology, evolution and historical biogeography have been mentioned independently by several prominent evolutionary ecologists, including Farrell *et al.* [31], Ricklefs and Schluter [18], Latham and Ricklefs [32], Futuyma [33] and Brown and Lomolino [1]. Unfortunately, this theory appears to have had little impact on research by ecologists and historical biogeographers, possibly because it has not been sufficiently emphasized in the literature. We elaborate this model here (Figure 1), focusing on the latitudinal gradient (the tendency for species richness to increase from poles to equator). The model combines three basic ideas:

- Many groups of organism that have high tropical species richness originated in the tropics and have spread to temperate regions either more recently or not at all. If a clade originated in the tropics then (all other things being equal) it should have more tropical species because of the greater time available for speciation in tropical regions to occur (i.e. the time-for-speciation effect [34]).
- One reason that many extant clades of organism originated in the tropics is that tropical regions had a greater geographical extent until relatively recently (~30–40 million years ago, when temperate zones increased in size [35]). If much of the world was tropical for a long period before the present, then (all other things being equal) more extant clades should have originated in the tropics than in temperate regions.
- Many species and clades are specialized for tropical climates, and the adaptations necessary to invade and persist in regions that experience freezing temperatures have evolved in only some. Tropical niche conservatism has helped maintain the disparity in species richness over time.

At least two lines of evidence support this tropical conservatism hypothesis. First, many groups of organisms that show the expected gradient in species richness also appear to show the predicted pattern of historical biogeography, with an origin in the tropics and more recent dispersal to temperate regions, including many angiosperm clades [36]. Similarly, analyses of New World birds reveal older average divergences among tropical taxa than among temperate ones [18,37], as predicted by this hypothesis (Figure 1).

Second, many distantly related groups show similar northern range limits, in spite of the lack of an obvious geographical barrier, suggesting that cold climate and niche conservatism act as barriers to the invasion of temperate zones by tropical clades. Thus, many neotropical

clades currently have their northern range limits in the tropical lowlands of Mexico [e.g. brazil nuts (Lecythidaceae), phyllomedusine treefrogs, boine snakes, tinamous, monkeys and sloths], whereas many other groups have their northern range limits in southern China and Vietnam (e.g. dipterocarp trees, rhacophorid frogs, pythonid snakes, broadbills and gibbons). These regions of biotic turnover in Mexico and Asia have not gone unnoticed; in fact, they correspond to borders between the global zoogeographical realms recognized by Wallace [38]. Furthermore, many of the groups involved are old (e.g. caecilian amphibians, which date back to the Jurassic [39]), suggesting that there has been ample time for invasion of temperate regions, but that their northward dispersion was limited by their inability to adapt to colder climates.

Similarly, many clades are widely distributed in tropical regions around the world but have never successfully invaded or radiated in temperate regions (e.g. modern cycads, palms, figs, onychophorans, caecilians, crocodiles, parrots, trogons and primates). This pattern again suggests that dispersal into temperate regions has not been prevented by either lack of time or limited dispersal ability, but instead by niche conservatism.

Advantages of the hypothesis

The tropical conservatism hypothesis is consistent with the results of many traditional ecological analyses of species richness (i.e. testing relationships between local richness and environmental variables) but it makes additional predictions that are unique. Similar to these correlational studies, the tropical conservatism hypothesis predicts high species richness in regions characterized by warm temperatures and abundant rainfall [29], given that these conditions characterized the ancestral niches of many clades. However, the tropical conservatism hypothesis also predicts differences in the relative ages and diversities of clades in tropical versus temperate regions (i.e. typically younger and less diverse clades in temperate regions), and major breaks in the geographical distribution of species and clades corresponding to particular shifts in climate (i.e. freezing temperatures).

Hypotheses based on niche conservatism (such as the tropical conservatism hypothesis outlined here) might help explain many other patterns of species richness besides the latitudinal gradient [1,18,33]. For a given group of organisms, the concept of niche conservatism predicts that habitats that are radically different from the ancestral niche will have more limited richness because of the inability of most lineages to colonize them (e.g. deserts, hot springs, oceans for terrestrial or freshwater organisms and vice versa). Among the many theories proposed to explain the latitudinal gradient, the niche conservatism hypothesis might be the only one capable of simultaneously explaining the high tropical richness of most groups and the reverse latitudinal gradient found in others (i.e. groups originating in temperate regions will colonize tropical regions rarely and more recently, with less time for speciation in the tropics [34]).

Problems with the hypothesis

So far, the predictions of the tropical conservatism hypothesis have not been rigorously tested, so empirical

support remains limited. Furthermore, in some groups, there might be shifts in diversification rate (speciation–extinction) associated with different areas; for example, some groups appear to have a faster rate of diversification in tropical regions [40]. This observation does not directly contradict the tropical conservatism hypothesis, but suggests that other processes drive the latitudinal gradient in these groups. For example, glaciation probably reduced species richness in some high latitude regions. Conversely, greater zonation of climatic regimes in tropical mountains might increase speciation in tropical montane regions relative to temperate ones [41], and there is evidence suggesting high rates of diversification in tropical and subtropical mountains [28]. We think that tropical conservatism contributes to higher species richness in tropical regions in general, but is not its sole cause in all groups.

Conclusions and prospects

We have attempted to characterize the current gulf between ecology and historical biogeography and the mutual benefits of greater integration between these fields. We see a need for a new research program to explain large-scale biogeographical patterns in a combined ecological and phylogenetic framework. This endeavor will require close collaboration between phylogeneticists and ecologists, and the development of new theory and statistical tools. We look forward to the translation of verbal arguments, such as the tropical conservatism hypothesis, into formal, testable models with parameters including ancestral niche, dispersal, speciation, extinction and time (along the lines of Hubbell's neutral theory [26]). In the meantime, however, there is much that can be done to bridge this gap. For example, phylogeneticists can begin to address many crucial issues, even if only limited ecological data are available. These issues include the amount of dispersal between climatic regimes and whether most temperate clades are recently derived from tropical ancestors. Conversely, ecologists can increase our understanding of the causes of large-scale biogeographical patterns by studying local and individual-scale ecological processes underpinning range limits of selected species from major clades [42]. They also can gain insight into community assembly and species richness patterns by considering the biogeographical history of the species and clades that make up these patterns. For example, reference to phylogenetic biogeographical hypotheses might identify which species and traits evolved *in situ* versus those that evolved elsewhere and moved into the community at a later date [43].

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