

# A phylogenetic perspective on the distribution of plant diversity

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**Phylogenetic studies are revealing that major ecological niches are more conserved through evolutionary history than expected, implying that adaptations to major climate changes have not readily been accomplished in all lineages. Phylogenetic niche conservatism has important consequences for the assembly of both local communities and the regional species pools from which these are drawn. If corridors for movement are available, newly emerging environments will tend to be filled by species that filter in from areas in which the relevant adaptations have already evolved, as opposed to being filled by *in situ* evolution of these adaptations. Examples include intercontinental disjunctions of tropical plants, the spread of plant lineages around the Northern Hemisphere after the evolution of cold tolerance, and the radiation of northern alpine plants into the Andes. These observations highlight the role of phylogenetic knowledge and historical biogeography in explanations of global biodiversity patterns. They also have implications for the future of biodiversity.**

biodiversity | niche conservatism | community assembly | historical biogeography | climate change

The rise of phylogenetic biology has revolutionized the study of molecular and developmental evolution, but has still had rather limited impact in ecology. Interest in phylogeny is growing within community ecology, but it has received almost no attention among ecosystem ecologists (however, see ref. 1). It is possible that knowledge of phylogeny is less relevant in these areas, but it seems more likely that the most productive intersections have not yet crystallized. Recent work on community phylogenetics, and emerging ideas on the integration of historical biogeography in studies of biodiversity, may be yielding a key principle governing the historical assembly of communities, which could in turn provide the basis for a new synthesis of phylogeny and ecology. Put simply, it may often be easier for lineages to move than it is for them to evolve. My essay is an attempt to better characterize this principle and explore some of its consequences for global diversity patterns and the future of biodiversity.

## Reflections on the Evolution of Ecological Traits

When I began studying phylogenetic systematics in the late 1970s, it was widely believed that ecologically important traits were too labile to be of much use in phylogenetic inference. The feeling was that such characters were so prone to homoplasy that they would be positively misleading about relationships; instead, one should concentrate on characters that lack obvious functional value [Mayr (2) called this the “Darwin principle”]. The rapid rise of the use of molecular data were partly a function of the belief that molecular characters were less subject to selection and would therefore better reflect evolutionary history. Arguments were made against this view on the grounds that it was hard to judge the phylogenetic value of characters at the outset of an analysis (e.g., see ref. 3). However, in general, such arguments had rather little impact on the overall mindset; homoplasy was viewed as bad for phylogenetics and “ecological traits” were viewed as especially prone to homoplasy.

Where did this view come from? Within systematic biology one line of reasoning was that groups that were placed at higher taxonomic ranks (e.g., families, orders) showed little uniformity

with respect to the environments that they occupied. This was said to be especially true in plants. For example, Arthur Cronquist, the prime architect of angiosperm classification in that era (from the 1960s through the 1980s), pointed out repeatedly that higher taxa were not readily characterized by particular ecological roles: “Each of the obvious ecological niches for land plants is occupied by species representing diverse families and orders. . . . Conversely, a single family may fill widely varying ecological niches” (4). Instead, higher taxa tended to be more uniform in minute details of their flowers and fruits, which remained constant through transitions into disparate environments. Cronquist referred especially to the Asteraceae (sunflower family) for support, noting that its members are marked by totally obvious reproductive characters, but vary from being trees, to shrubs, vines, succulents, and perennial and annual herbs, which grow from tidal to alpine zones, from the equator nearly to the poles. He concluded from such cases that “. . . the obvious adaptive changes that can take place mostly occur so easily and frequently that they tend to mark species and genera rather than larger groups” (4).

Ledyard Stebbins, whose 1974 book (5) on the macroevolution of flowering plants dominated discussions for decades, held much the same view. That is, he argued that owing ultimately to limited functional and developmental integration in plants, vegetative traits related to climate tolerances were highly labile and only rarely marked higher taxa. In fact, his main thesis depended directly on the rapidity with which transitions between major climate zones could occur. He argued that major evolutionary changes occurred in ecotones or climatically marginal zones, and that tropical rain forests were therefore “museums,” not “cradles.” As he appreciated, this required “extreme ecological plasticity” and genetic adaptation to moister or drier climates with “relative ease” (5).

Growing up with these views, and having passively accepted them, I remember being surprised by several later findings. Whereas I fully expected reproductive traits to show less homoplasy than vegetative traits that seemed to be linked more directly to climate variables (e.g., leaf margins, pubescence), a metaanalysis of homoplasy in published plant phylogenies failed to demonstrate such a difference (6). In fact, levels of homoplasy in phylogenetic studies rarely seem to correspond to standard intuitions about lability or selective value. Instead, homoplasy seems to be positively correlated primarily with the number of terminal taxa included in analyses (e.g., ref. 7) and limitations on the number of character states (8).

Even more surprising was the finding by Campbell Webb (9) that the trees occupying 0.16-hectare plots in a rainforest in Borneo seemed to be more closely related to one another than

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expected by chance assembly from the regional species pool of 324 tree species. Given that these plots differed with respect to key environmental variables (some were located in swampy areas, some on ridge tops, etc.), one interpretation is that there are subtle, previously underappreciated, ecological similarities among related plants, both above and below the traditional rank of family. In retrospect, this can be reconciled with Cronquist's observations simply by allowing that shared ecological niche characteristics exist, but that the phylogenetic distribution of these does not correspond well with particular named clades or taxa assigned to a given taxonomic rank.

In general, comparisons centered on taxonomic ranks have hidden the connections between phylogeny and ecology. In fact, some traditional taxonomic families are generally associated with particular environments; for example, Poaceae (the grasses) in grasslands, Ericaceae (the heaths) in heathlands, and Zosteraceae (the sea grasses) in the sea. The plant clade I know the best, the Dipsacales, ancestrally occupied northern temperate forests, but Dipsacaceae have specialized in drier habitats, especially around the Mediterranean basin, and Valerianaceae have adapted to alpine habitats (10). But there are also ecologically distinctive clades within traditional families: multiple mangrove lineages, dry-adapted Euphorbiaceae, and bamboos and multiple C4 lineages within grasses, to name just a few examples. Likewise, there are ecologically distinguishable clades comprised of a number of related families. Core Caryophyllales provide an example, mostly being adapted to arid or high salinity habitats (e.g., the "portulacaceous alliance" of families, which includes the Cactaceae). The several insectivorous families within Caryophyllales *sensu lato* present another clear case, as do those of the "aquatic clade" within Alismatales, and the parasitic plants of Santalales.

Moreover, it is important to appreciate that the findings of Webb (9) and others (see below) do not depend on all members of a clade occupying the same habitat, but rather on a tendency for members of a clade to be more similar with respect to the environments that they occupy. From this perspective the link between phylogeny and ecology becomes even more clear. After all, major clades within angiosperms, despite significant ecological diversity, hardly occupy all possible environments, but instead are restricted to one or a few major biomes, such as tropical rain forests, temperate forests, grassland, or deserts. Despite the great variety of environments occupied by the Asteraceae, for example, they are far more common in arid environments than they are in tropical forests. Such tendencies are well known to field botanists, but have only recently been subjected to analysis. In the most comprehensive study to date, Prinzing *et al.* (11) demonstrated far higher than expected levels of niche conservatism in the plants of central Europe.

Such ecological correlations (especially those at the level of major clades) imply that evolutionary shifts from one ecological setting into another, where these require substantial physiological adjustments, are not so readily accomplished as one might have imagined, homoplasy in ecological traits notwithstanding. Consider one example: the evolution of cold tolerance. Many plant lineages have managed to adapt to cold, highly seasonal climates, but it is also true that only a subset of ancestrally tropical plant lineages have succeeded in making this transition (12). That is, many tropical plant groups are strictly tropical (e.g., half of the families of flowering plants have no temperate representatives; ref. 13) and have not spread out of the tropics despite presumably having had ample opportunity to do so with the expansion of temperate climates (or the contraction of the tropics) during the Tertiary (14). The implication is that it is not so easy to evolve tolerance to freezing temperatures and highly seasonal environments. In fact, such adaptations do appear to require a coordinated set of physiological adjustments, including

(in most cases) biochemical changes to maintain a fluid lipid layer for the rapid transfer of water out of cells to avoid ice crystals forming in the cytoplasm, and the deployment of special proteins and sugars to stabilize membranes when cells become desiccated and condensed (15, 16).

Overall, my impression of ecological traits is that they show the same wide range in evolutionary lability as do morphological traits. On one end of the spectrum there are extremely labile traits of the sort that ecologists and population geneticists have tended to concentrate on. On the other end there are ecological traits of the sort I have highlighted above, which are evolutionarily much more conserved, perhaps because their evolution entails the modification of complex, highly integrated physiological systems. Recent phylogenetic studies have simply focused new light on the existence and the global importance of key ecological traits at the more conservative end of this distribution. My concentration here on the conserved end of the distribution is in no way meant to question the reality or significance of highly labile ecological traits, the evolution of which surely underlie many ecological adjustments.

### Phylogenetic Niche Conservatism (PNC)

What Harvey and Pagel (17) termed PNC refers to the expectation that, all else being equal, related species will tend to occupy the same sorts of environments (18). PNC is not meant to imply that ecological barriers are insurmountable, or even that niche shifts are rare. Niche evolution obviously occurs, and may even be the norm under certain circumstances (e.g., ref. 19). However, PNC, to the extent that it exists, does imply that speciation can occur regularly without major niche shifts (e.g., ref. 20). Furthermore, under the assumption that opportunities to undergo major shifts have regularly presented themselves, PNC implies that these opportunities have not been seized so readily that high-level eco-phylogenetic correlations are completely overridden by ongoing low-level niche shifting. Although, strictly speaking, it is not necessary to link PNC with the view that there are constraints on niche evolution, I believe that it is the relative difficulty of making major ecological shifts that explains the patterns I have highlighted above, and which, as discussed below, render PNC especially consequential in explaining the distribution of biodiversity.

An example of the potentially significant role that PNC plays in structuring the distribution of biodiversity relates to discussions of the latitudinal species diversity gradient (reviewed by Mittlebach *et al.*, ref. 21). One long-standing hypothesis has been that this pattern is underlain by a simple historical cause, namely a longer time for diversification in the tropics in many lineages than outside of the tropics. If many extant lineages originated and began their diversification under tropical climatic conditions, and if movements of these lineages out into temperate climates occurred only more recently, this alone would go a long way toward explaining the gradient (e.g., refs. 22–25). Rangel *et al.* (26) put this verbal argument to the test in a simulation focused on bird biodiversity in South America, showing that realistic patterns can be obtained under a variety of circumstances.

A key ingredient of this argument, which led John Wiens and I to call it the "tropical niche conservatism" hypothesis (24), is that not all tropical lineages confronted with the retraction of tropical climates during the Tertiary managed to adapt to colder climates. Instead, many of these lineages simply tracked tropical habitats, and therefore became increasingly geographically restricted. If every tropical lineage had been able to readily adjust to cold temperatures and extreme seasonality, then the latitudinal diversity gradient would be far less steep than the one we observe today. This is the important sense in which PNC has explanatory power beyond the time-for-speciation factor.

### Niche Conservatism and Local Community Assembly

That there should exist a general relationship between phylogenetic relatedness and ecological interactions that are crucial to community assembly, has been evident from Darwin (27) onward. As G. Evelyn Hutchinson put it in 1965 (28): “It is evident that at any level in the structure of the biological community there is a set of complicated relations between species, which probably tend to become less important as the species become less closely allied. These relations are of the kind which ensure niche separation.” With the rapid expansion of phylogenetic knowledge (e.g., see ref. 29), it has now become possible to study this rigorously.

A series of recent analyses imply that PNC influences community composition both by the filtering of the regional species pool based on abiotic niche parameters and through competition and other biotic interactions. The signals of these processes may be reflected in the distribution of species across the phylogeny of the regional species pool (quantified using a variety of phylogenetic diversity measures; refs. 9, 30, and 31; www.phylodiversity.net/phylocom). As Webb *et al.* (32) and Cavender-Bares and Wilczek (33) reasoned, where abiotic habitat filtering is the dominant force shaping coexistence, PNC should result in phylogenetic clustering in the phylogeny of the regional species pool. On the other hand, where biotic competitive exclusion is the dominant ecological force, PNC should result in a more even (overdispersed) distribution of species on the regional tree than expected by chance.

These relations may hold in the abstract, and have oriented the interpretation of a number of studies (e.g., refs. 34–36), but there are a variety of complications or necessary extensions. For example, as Webb *et al.* (32) and Cavender-Bares and Wilczek (33) appreciated, an overdispersed phylogenetic pattern can also result from abiotic filtering from an underlying phylogeny showing convergent niche evolution. This observation simply highlights the need to couple such studies with independent phylogenetic tests of the extent of PNC in the clades under consideration (cf. refs. 36 and 37). Likewise, “ecological facilitation,” rather than competition, might underlie an overdispersed phylogenetic pattern (38), again emphasizing that there is not a simply one-to-one relationships between a phylogenetic pattern and an underlying cause.

It is also clear that possible causal processes will vary in intensity, and even in kind, as a function of scale (39). For example, Webb *et al.* (40) hypothesized that seedling phylodiversity patterns within small rain forest plots reflect the sharing of fungal pathogens among close relatives, whereas at a larger scale in the same forest they found evidence of habitat filtering. Cavender-Bares *et al.* (34, 37), in studies centered on oaks (*Quercus*) in Northern Florida, showed evidence for phylogenetic evenness at smaller spatial and taxonomic scales (interpreted as the outcome of competition), but phylogenetic clustering at larger scales (interpreted as habitat filtering of phylogenetically conserved ecological traits). Clearly, sorting out among such possibilities requires the development of appropriate null models, and simulations to evaluate the power to distinguish alternative explanations (e.g., refs. 41 and 42).

For present purposes it is especially important to note that entirely different causal factors become relevant as such studies scale up to much broader regions, or focus on clades that have moved around the globe. For example, Forest *et al.* (43) reported lower phylogenetic diversity (despite higher species diversity) in the western Cape flora of South Africa, in part as a function of multiple rapid radiations (44). In contrast, the eastern Cape showed higher phylodiversity, in part because it interdigitates with another biodiversity hotspot. The key point is that at such larger scales historical factors such as speciation, extinction, and biogeographic boundaries become highly relevant.

### Niche Conservatism and Regional Species Pools

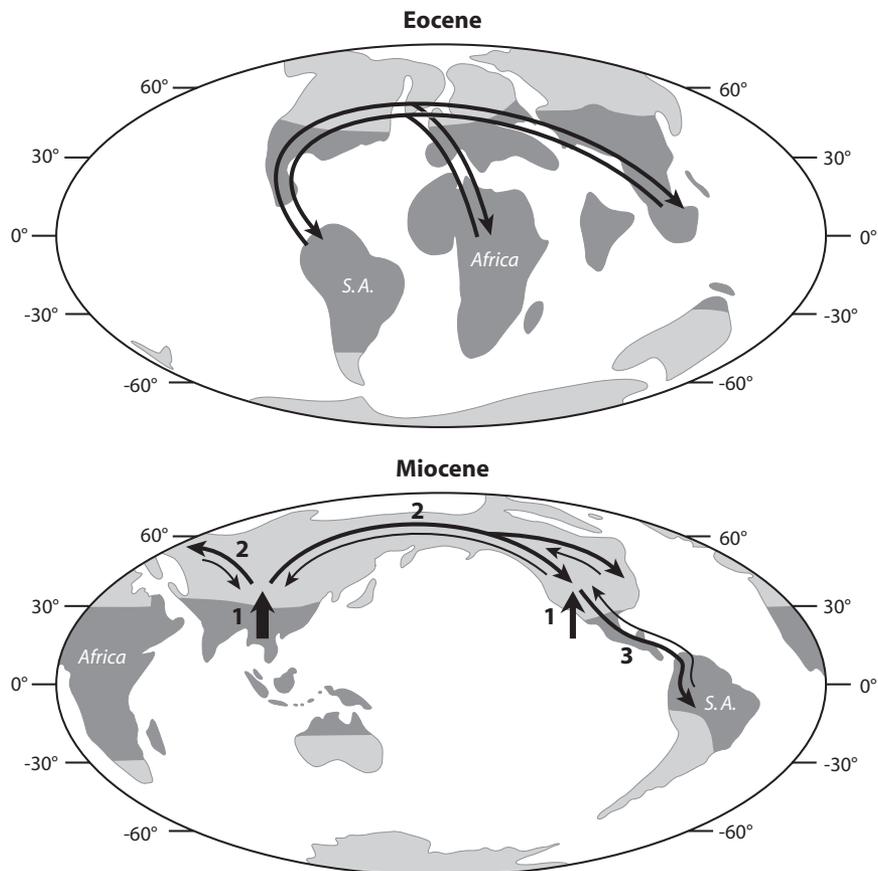
A less well appreciated role of phylogenetic niche conservatism, and the one that I especially want to highlight here, concerns the composition of the regional species pools from which local communities become assembled. In my view the most compelling studies to date along these lines have been carried out in Mediterranean climate systems, by Miguel Verdu *et al.* (45) and David Ackerly (46), both building on the seminal work of Carlos Herrera (47).

I will focus here on Ackerly (46), as his study concerned a single region, the California chaparral. His analyses of a number of signature woody chaparral clades suggested that in many cases the characteristic adaptive traits were evolved well before the advent of the Mediterranean (summer dry) climate some 3 million to 5 million years ago. Plants with these characters (or their similar precursors) were either present in the vegetation of that region beforehand, or they moved in from outside the region, perhaps from dry areas further to the east and south (“mexical” vegetation), as opposed to evolving *in situ* in response to the changing climate. That is, many characteristic elements of the flora (e.g., *Ceanothus*, *Arctostaphylos*), and consequently many of the traits that we associate with chaparral (e.g., thick, sclerophyllous leaves), resulted from the sorting of species with relevant adaptations already in place, which then adjusted to the new rainfall regime by shifts in the timing of growth and reproduction. In a few lineages (e.g., *Adenostoma*, *Heteromeles*), however, chaparral leaf features probably did evolve *in situ*. Interestingly, many of the elements that filtered into the flora have Madrean-Tethyan affinities (48) and were preadapted to hotter, arid conditions, whereas those showing *in situ* adaptation derive mainly from temperate Northern Hemisphere lineages. In other words, it appears that the composition, structure, and function of the chaparral as we know it today reflects the characteristics of prechaparral vegetation and the biogeographic source areas that were accessible as the climate materialized.

### It's Easier to Move Than to Evolve (Unless It Isn't)

These studies suggest what may be a general principle, namely that under many circumstances it may be easier for species to migrate into an area with at least some of the relevant adaptations having already evolved, than it is for those adaptations to evolve in place. This formulation highlights two key variables, namely the rate of trait evolution in relation to the rate of dispersal. But, the existence of relevant geographic/climatic connectivities through the relevant time period is critical to the general model and to specific outcomes. If, when climate change occurs, suitable corridors exist for the dispersion of species with relevant traits, these lineages will tend to track the habitat to which they are adapted and move into the region relatively quickly, perhaps preempting the *in situ* evolution of these traits among the natives. Under these circumstances, it is the sorting or filtering of species into the region that will dominate the assembly of the regional species pool.

On the other hand, if plants with relevant adaptations do not already exist in an area undergoing environmental change, and if corridors for the movement of relevant plants are missing at the right times and places, then adaptations will presumably evolve within the resident lineages. Oceanic islands, of course, provide classic cases of such isolation and of the ecological radiations of those species that did manage to establish (e.g., refs. 49 and 50). But, as Ackerly (51) has argued, isolation by distance can also occur in continental settings (e.g., isolated mountaintops, peculiar edaphic circumstances), and “environmental islands” that are discontinuous in realized environmental space from surrounding habitats can similarly promote adaptive divergence.



**Fig. 1.** Major patterns in the movement of plant lineages discussed here. (*Upper*) Hypothesized movements in both directions of now disjunct tropical lineages across the North Atlantic during the early Tertiary. (*Lower*) (1) Hypothesized originations of adaptation to cold, seasonal climates, perhaps predominantly in Asia. (2) Iterated movement more recently of temperate lineages around the Northern Hemisphere, especially through Beringia, and perhaps predominantly out of Asia. (3) More recent New World movements of lineages adapted to high elevations, especially from North America into the Andes of South America over the last 5 million years. Base maps for the Eocene ( $\approx 50$  million years ago) (*Upper*) and the Miocene ( $\approx 14$  million years ago) (*Lower*) are based on C. R. Scotese's PALEOMAP Project ([www.scotese.com](http://www.scotese.com)). Darker gray areas show the hypothesized distribution of tropical climates during those time periods (see ref. 14).

Major physiological/morphological adaptive shifts certainly have occurred, sometimes frequently, and sometimes even rapidly, perhaps especially in relative isolation. My argument is that under circumstances of habitat continuity that promote migration, movement into an area experiencing change is often likely to occur before resident species adapt to the circumstances. It is a question, then, of the interplay of historical circumstances either favoring or disfavoring the movement of lineages from habitats outside of a region, with the relative ease or difficulty of evolving the suitable ecological characters. If movement into the area is difficult, and the relevant adaptive shifts are easy, then *in situ* evolution will predominate. My assertion is simply that corridors have often been present, and that adaptations to major new climates have often been somewhat difficult.

The existence of corridors at the right times and places not only provides a mechanism for community assembly but also helps to explain PNC itself. Under these circumstances, stabilizing selection may be a key factor in maintaining ecological tolerances. If corridors did not exist and isolation were correspondingly increased, *in situ* evolution and local extinction would probably increase and PNC would be less commonly observed. That is, there is a connection between environmental connectivity and niche conservatism, on the one hand, and between isolation and convergent ecological adaptation on the other (*cf.* ref. 52). In this sense, historically contingent connectivities have played a more central role than we might have imagined in mediating the tradeoff of dispersal and evolutionary change,

and, thereby, in generating the patterns of biodiversity that we see today.

A key question that has still received only limited attention, concerns the circumstances in addition to isolation that will favor adaptive niche evolution. Ackerly (51), for example, highlighted the evolutionary opportunities that may present themselves along the "trailing edge" of a species that is shifting its geographic range in response to changes along a single environmental axis (e.g., temperature). This mechanism depends to some extent on a barrier preventing immediate occupancy by species that are appropriately adapted to the new conditions. Here, too, it is the balance of the ease of movement in relation to the ease of adaptation that determines the outcome.

### Three Examples

I believe that the simple idea outlined above provides the basis for a much fuller understanding of global biodiversity patterns, and that phylogeny and PNC will therefore play a much larger role in explaining such patterns. Here, I briefly highlight three biodiversity phenomena in flowering plants that variously reflect the interaction of niche conservatism with environmental changes through the Tertiary (Fig. 1).

The first example concerns the disjunction of clades among the major tropical regions of the world. Although many of these cases, especially involving South America and Africa, have traditionally been attributed to the break up of Gondwana, recent studies have shown that in many (perhaps most cases) the

relevant lineage-splitting events are too young. Instead, there must have been movements among these regions after the break-up was well along. An example is provided by Malpighiaceae, which is most diverse in the New World tropics but has several lineages in tropical Africa (and Madagascar) and Asia. Analyses by Davis *et al.* (53, 54) demonstrated that this distribution reflects several disjunctions, in widely separated clades, and that these were, on the whole, too young to have been caused by the spreading of the Atlantic. The presence of fossils in several places in the Northern Hemisphere, where Malpighiaceae no longer occur, combined with evidence on paleogeography and the greatly expanded northern limit of tropical climates and vegetation in the Eocene (e.g., ref. 14), favor the movement of several lineages from the New World tropics into the Old World tropics through a Laurasian corridor of tropical climates in the early Tertiary.

The modern disjunct distribution is largely, therefore, a result of the southward retreat of these plants as tropical climates receded in the Oligocene and Miocene. The key point is that, perhaps despite “trailing edge” opportunities, these plants maintained their tropical physiological tolerances and moved out of northern regions as climates shifted, as opposed to adapting to colder, seasonal climates and maintaining a northern distribution. The same sort of explanation, involving tropical niche conservatism, applies to other major tropical disjunctions, including subgroups within Melastomataceae (55) and Lauraceae (56), the latter probably moving from east to west through the boreotropics (for possible additional examples see refs. 57–60).

A second example is in some ways a mirror image of the first. This concerns plants that were able to adapt to cold, highly seasonal environments in the north. The lineages that did manage this transition were able to move (often repeatedly and at different times) around the Northern Hemisphere, especially as a major corridor through Beringia opened and closed with fluctuating climates (61). Ultimately, these movements yielded the very common disjunctions between the temperate forests of eastern Asia and eastern North America (62–64).

Here, too, it is important to appreciate the dual role played by PNC. First, recall that only some originally tropical lineages managed to make the transition to temperate climates (12, 23). Malpighiales provide an example (65). As noted above, Malpighiaceae remained restricted to tropical climates, and the same is true of most other major lineages within Malpighiales. Only a few lineages made it out of the tropics and have been successful in the northern temperate zone, including violets (Violaceae), willows (Salicaceae), and St. John’s worts (Hypericaceae). As suggested above, this may relate to the complexity of the cell-level adaptations necessary to tolerate frost. Second, just as only some tropical lineages adapted to temperate climates, only some temperate plant lineages adapted to even colder climates that would have allowed their continuous distribution through Beringia, even today. It is also noteworthy that few temperate-adapted plant lineages appear to have moved back into truly tropical climates, although in this case competition may also have played an important role.

One final aspect of this case is noteworthy. There is still little phylogenetic evidence for the argument (see ref. 23) that the majority of transitions from the tropics into the Northern temperate zone took place in Asia. However, it is noteworthy that “out of Asia” biogeographic inferences have been the most commonly reported to date and appear to well outnumber originations in North America and subsequent movement to Asia (64). The continuous connection that existed in Asia between tropical and temperate climates and vegetation types throughout the Tertiary, and the great complexity of the landscape, may have promoted both the generation and the maintenance of higher species diversity in eastern Asia as compared with North America or Europe (23, 66–68).

My third example concerns plants adapted to high-elevation alpine conditions. Historical biogeographic analyses of several clades that have succeeded in mountainous areas around the world indicate that these originated in the Northern Hemisphere, often in Asia, moved around the Northern hemisphere, and then, much more recently, moved into South America, where they have radiated in the Andes. Valerianaceae provide an example (69, 70). These plants appear to have originated in the Himalayas, to have moved to North America, and then into South America, perhaps on the order of 6 million to 8 million years ago, not long before the physical connection was established. In the Andes there are now  $\approx 150$  species of *Valeriana sensu lato*. Similar patterns of movement and diversification have been documented in *Gentianella* (71), *Halenia* (72), and *Lupinus* (73), to name a few cases.

Two aspects of this case warrant comment. First, this pattern provides perhaps the clearest case of the movement of pre-adapted plants into a region as physical changes created new climates. Owing to the formation of the corridor and the dramatic rise of the Andes in the same timeframe, movement into these habitats was evidently easier than the evolution of alpine adaptations *in situ*. However, it remains unclear how many resident South American plant lineages living at lower, warmer elevations, gave rise to Andean alpine plants (e.g., *Espeletia*, Asteraceae; *Puya*, Bromeliaceae). Second, it is noteworthy that a number of these movements into the Andes appear to have been accompanied by an upward shift in diversification rate. One obvious factor is geographical complexity and its promotion of allopatric speciation, at least in part as a function of PNC (74). But, another important factor may have been the relative lack of occupancy by South American plants, owing in part to the relative difficulty of evolving the necessary traits *in situ*. In exploring this case further, however, it will be important to bear in mind differences between adapting to tropical highlands versus cold climates at high latitudes (see refs. 16, 75, and 76).

### Concluding Thoughts

Explanations for major patterns in the distribution of biodiversity have traditionally tended to focus on environmental correlations and local determinism. With the rapid rise of phylogenetic knowledge, a growing appreciation of the extent and possible roles of phylogenetic niche conservatism, and the development of better analytical tools, especially to infer historical biogeography (e.g., ref. 77) and rates of diversification (e.g., ref. 78 and see ref. 79), the stage is clearly set to reintegrate historical factors into such explanations. These are in no way meant to replace environmental explanations, but rather to complement them and connect them to the speciation, extinction, and migration processes that ultimately underlie such patterns (24).

The argument I am making in several ways parallels the view set out by Gould and Lewontin in 1979 (80) on the study of adaptation. They argued that adaptation is caused not by the environment, but by the interaction of the environment with the evolved, organismic substrate. They viewed the substrate in this interaction as determining the outcome just as much as the environmental pressures and argued that these should be treated as equal partners in the causal explanation. Likewise, I am arguing that it is the action of changing environments on the evolved ecological characteristics of lineages that results in the patterns of biodiversity we observe today, and, furthermore, that the role that these lineages play is every bit as interesting and powerful in determining the outcome. In short, I am agreeing with Robert Ricklefs (81) that we should “raise regional and historical factors to equal footing with local determinism in their influence on the diversity–environment relationship and geographical patterns of diversity in general.” Fortunately, whereas the integration of phylogenetic knowledge into such explana-

tions once seemed unnecessary, and for a time seemed interesting but impractical, now it seems virtually inevitable.

Finally, it is worth reflecting on the future of biodiversity in light of the basic principle highlighted here. In the deep evolutionary past, corridors for the movement of biotas within and among continents were opened or shut based primarily on the relative position of landmasses, geologic particulars (e.g., the location and orientation of rivers and mountain ranges), and climate changes. Moving into the future, anthropogenic habitat fragmentation adds a complicating new variable to the equation, as does the current rapidity of climate change and the wholesale movement of species by humans. Depending on the vagility of the organisms involved, the habitat discontinuities imposed by humans may limit the impact of the migration of preadapted species in community assembly, which I believe has played such an important role in the past. The consequences for community composition, structure, and function are unclear. One possibility is that anthropogenically isolated habitats will remain, at least for a time, “empty” of species from surrounding areas that might be well adapted to them. On the other hand, barriers to migration might create circumstances that favor niche shifts in the resident species (cf. ref. 51). Then again, such changes would be counterbalanced by probable reductions in genetic diversity and human species introductions.

- Edwards EJ, Still CJ, Donoghue MJ (2007) The relevance of phylogeny to studies of global change. *Trends Ecol Evol* 22:243–249.
- Mayr E (1969) *Principles of Systematic Zoology* (McGraw-Hill, New York).
- Hennig W (1966) *Phylogenetic Systematics* (Univ Illinois Press, Urbana).
- Cronquist A (1968) *The Evolution and Classification of Flowering Plants* (Houghton Mifflin, Boston).
- Stebbins GL (1974) *Flowering Plants: Evolution Above the Species Level* (Belknap, Cambridge, MA).
- Donoghue MJ, Sanderson MJ (1994) in *Homology: The Hierarchical Basis of Comparative Biology*, ed Hall B (Academic, San Diego), pp 393–421.
- Sanderson MJ, Donoghue MJ (1989) Patterns of variation in levels of homoplasy. *Evolution (Lawrence, Kans.)* 43:1781–1795.
- Donoghue MJ, Ree RH (2000) Homoplasy and developmental constraint: A model and an example from plants. *Am Zool* 40:759–769.
- Webb CO (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am Nat* 156:145–155.
- Donoghue MJ, Bell CD, Winkworth RC (2003) The evolution of reproductive characters in Dipsacales. *Int J Plant Sci* 164:5453–5464.
- Prinzinger A, Durka W, Klotz S, Brandl R (2001) The niche of higher plants: Evidence for phylogenetic conservatism. *Proc R Soc London Ser B* 268:2383–2389.
- Judd WS, Sanders RW, Donoghue MJ (1994) Angiosperm family pairs: Preliminary phylogenetic analyses. *Harvard Papers Bot* 5:1–51.
- Ricklefs RE, Renner SS (1994) Species richness within families of flowering plants. *Evolution (Lawrence, Kans.)* 48:1619–1636.
- Fine PVA, Ree RH (2006) Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *Am Nat* 168:796–804.
- Sakai A, Larcher W (1987) *Frost Survival of Plants: Responses and Adaptation to Freezing Stress. Ecological Studies* 62 (Springer, Berlin).
- Körner C (2003) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems* (Springer, Berlin), 2nd ed.
- Harvey PH, Pagel M (1991) *The Comparative Method in Evolutionary Biology* (Oxford Univ Press, Oxford).
- Wiens JJ, Graham CH (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu Rev Ecol Syst* 36:519–539.
- Losos JB, et al. (2003) Niche lability in the evolution of Caribbean lizard communities. *Nature* 424:542–545.
- Peterson AT, Soberon J, Sanchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267.
- Mittelbach GG, et al. (2007) Evolution and the latitudinal diversity gradient: Speciation, extinction, and biogeography. *Ecol Lett* 10:315–331.
- Farrell BD, Mitter C, Futuyma DJ (1992) Diversification at the insect–plant interface. *Bioscience* 42:34–42.
- Latham RE, Ricklefs RE (1993) in *Species Diversity in Ecological Communities*, eds Ricklefs RE, Schuller DE (Univ Chicago Press, Chicago), pp 294–314.
- Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology, and species richness. *Trends Ecol Evol* 19:639–644.
- Jablonski D, Roy K, Valentine JW (2006) Out of the tropics: Evolutionary dynamics of latitudinal diversity gradients. *Science* 314:102–106.
- Rangel TFLVB, Diniz-Filho JAF, Colwell RK (2007) Species richness and evolutionary niche dynamics: A spatial pattern-oriented simulation experiment. *Am Nat* 170:602–616.
- Darwin C (1859) *On the Origin of Species* (Murray, London).
- Hutchinson GE (1965) *The Ecological Theater and the Evolutionary Play* (Yale Univ Press, New Haven, CT), pp 26–77.
- Cracraft J, Donoghue MJ, eds. (2004) *Assembling the Tree of Life* (Oxford Univ Press, New York).
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61:1–10.
- Webb CO, Ackerly DD, Kembel SW (2007) Phylocom: Software for the analysis of community phylogenetic structure and trait evolution. Version 3.41.
- Webb CO, Ackerly DD, McPeck M, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol Syst* 33:475–505.
- Cavender-Bares J, Wilczek A (2003) Integrating micro- and macroevolutionary processes in community ecology. *Ecology* 84:592–597.
- Cavender-Bares J, Ackerly DD, Baum DA, Bazzaz FA (2004) Phylogenetic overdispersion in Floridian oak communities. *Am Nat* 163:823–843.
- Ackerly D, Schwilk W, Webb CO (2006) Niche evolution and adaptive radiation: Testing the order of trait divergence. *Ecology* 87:550–561.
- Slingsby JA, Verboom GA (2006) Phylogenetic relatedness limits co-occurrence at fine spatial scales: Evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape floristic region, South Africa. *Am Nat* 168:14–27.
- Cavender-Bares J, Keen A, Miles B (2006) Phylogenetic structure of Floridian plant communities depends on spatial and taxonomic scale. *Ecology* 87:5109–5122.
- Valiente-Banuet A, Verdu M (2007) Facilitation can increase the phylogenetic diversity of plant communities. *Ecol Lett* 10:1029–1036.
- Swenson NG, Enquist BJ, Thompson J, Zimmerman JK (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88:1770–1780.
- Webb CO, Gilbert GS, Donoghue MJ (2006) Phylodiversity dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology* 87:5123–5131.
- Kraft NJB, Cornwell WK, Webb CO, Ackerly DD (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am Nat* 170:271–283.
- Kembel SW, Hubbell SP (2006) The phylogenetic structure of neotropical tree communities. *Ecology* 87:586–599.
- Forest F, et al. (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445:757–760.
- Linder HP (2005) Evolution of diversity: The Cape flora. *Trends Plants Sci* 10:536–541.
- Verdu M, Davila P, Garcia-Fayos P, Flores-Hernandez N, Valiente-Banuet A (2003) “Convergent” traits of Mediterranean woody plants belong to pre-Mediterranean lineages. *Biol J Linn Soc* 78:415–427.
- Ackerly DD (2004) Adaptation, niche conservatism, and convergence: Comparative studies of leaf evolution in the California chaparral. *Am Nat* 163:654–671.
- Herrera CM (1992) Historical effects and sorting processes as explanations for contemporary ecological patterns: Character syndromes in Mediterranean woody plants. *Am Nat* 140:421–446.
- Axelrod DI (1975) Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. *Ann Missouri Bot Gard* 62:280–334.
- Carlquist SJ (1974) *Island Biology* (Columbia Univ Press, New York).
- Baldwin BG, Sanderson MJ (1998) Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proc Natl Acad Sci USA* 95:9402–9406.
- Ackerly DD (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int J Plant Sci* 164:5165–5184.

If attention is focused on ecological traits that are highly labile, and likely to evolve quite rapidly, optimism about *in situ* adjustments may well be warranted. My basic argument is that it is important to appreciate that some ecological traits are far less likely to evolve rapidly, and that this conservatism has consequences. As we proceed to predict responses to global change, I believe it will be necessary to acknowledge and more finely characterize the spectrum that exists in the evolutionary lability of ecologically relevant traits. Ironically, however, we are rapidly creating genuinely unparalleled circumstances in which it is becoming difficult to apply our expanding knowledge of the past to predict the future. In this very important sense, it is becoming increasingly unclear what lies ahead for biodiversity.

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