Biome Shifts and Niche Evolution in Plants

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Abstract

What factors influence whether a lineage can successfully transition into a new biome, and why have some biome shifts been more frequent than others? To orient this line of research we develop a conceptual framework in which the likelihood of a biome shift is a function of (*a*) exposure to contrasting environments over time, (*b*) the evolutionary accessibility of relevant adaptations, and (*c*) changing biotic interactions. We evaluate the literature on biome shifts in plants in relation to a set of hypotheses on the size, connectedness, and absolute age of biomes, as well as on the adaptability of particular lineages and ecological interactions over time. We also critique the phylogenetic inference of past biomes and a "global" model-based approach to biome evolution. More robust generalizations about biome shifts will require detailed studies of well-sampled and well-resolved clades, accounting for changes in the relevant abiotic and biotic factors through time.

INTRODUCTION

In *The Geography of the Flowering Plants*, Ronald Good enumerated what he considered to be the fundamental rules governing plant geography (Good 1974, first published in 1947). He viewed climate change as the major driver of plant distributions and plant migration as the prime consequence of such change. Likening climate change to the engine of a locomotive and migration to its wheels, what was it, he asked, that played the role of the connecting rod—the part that translates the reciprocating motion of the pistons into the rotating motion of the wheels? It was, he answered, organismal tolerances:

> . . . the necessary connecting rod is provided in the form of a rigid relation between the species and the conditions under which it can exist. This relationship prevents the species from staying where it is and modifying its existence to the new surroundings which the movement of climate values (climate change) has brought about. (Good 1974, p. 449).

Here we recognize an early formulation of the concept of niche conservatism, which has attracted so much recent attention (Wiens & Donoghue 2004, Wiens & Graham 2005, Losos 2008, Wiens et al. 2010, Crisp & Cook 2012). Lineages fail to evolve in situ as environments change and instead track their habitats when possible or contract and develop disjunctions in their geographic ranges. It may be "easier to move than to evolve" (Donoghue 2008, pg. 11551).

Although it is undeniable that niche conservation has been important in shaping the distribution of biodiversity, how rigid has the connecting rod of tolerance really been? Many lineages have managed to adapt as environments have changed, for even the most recently formed biomes are occupied. Granting the existence and the significance of both responses—niche conservation and niche evolution—the question becomes: What are the factors that determine these different outcomes?

We are by no means the first to review this area (e.g., Wiens & Graham 2005, Wiens et al. 2010, Crisp & Cook 2012), but earlier efforts have focused more on documenting niche conservatism. Here we reorient the discussion around evolutionary changes that have allowed lineages to transcend biome boundaries—we refer to these as biome shifts. This reflects our belief that it may be more productive at this stage to concentrate on evolutionary change rather than evolutionary stasis. Of course, like many keywords in biology, "biome" is a fuzzy concept, but it is intended to capture how key climatic conditions are associated with characteristic biotic assemblages (**Figure 1**). Often, though not always, biome shifts entail adaptations associated with contrasting climates and/or vegetation types (e.g., closed canopy forest versus open grassland). Until recently, biomes have mainly been studied by ecologists, climatologists, and vegetation modelers, who have puzzled over their boundaries and the processes that form and maintain them (e.g., Staver et al. 2011, Hoffmann et al. 2012, Lehmann et al. 2014). Yet, as we discuss below, there are compelling evolutionary questions related to the formation of biomes—questions that can potentially be answered with the tools that are now at our disposal.

Our main realization is the need for a conceptual framework to orient this area of research. Although we can trace a thread of important contributions to this theory (e.g., Herrera 1992, Ackerly 2003, Ricklefs 2004, Wiens & Donoghue 2004, Pennington et al. 2006, Futuyma 2010), much remains to be done. And, in the absence of such a framework, we fear that this literature will remain little more than the sum of its largely incomparable parts. Reflecting our own limited expertise, we concentrate here on plants and on the relevant phylogenetic and biogeographic literature. Although other fields, including physiology, paleontology, and genetics, are highly
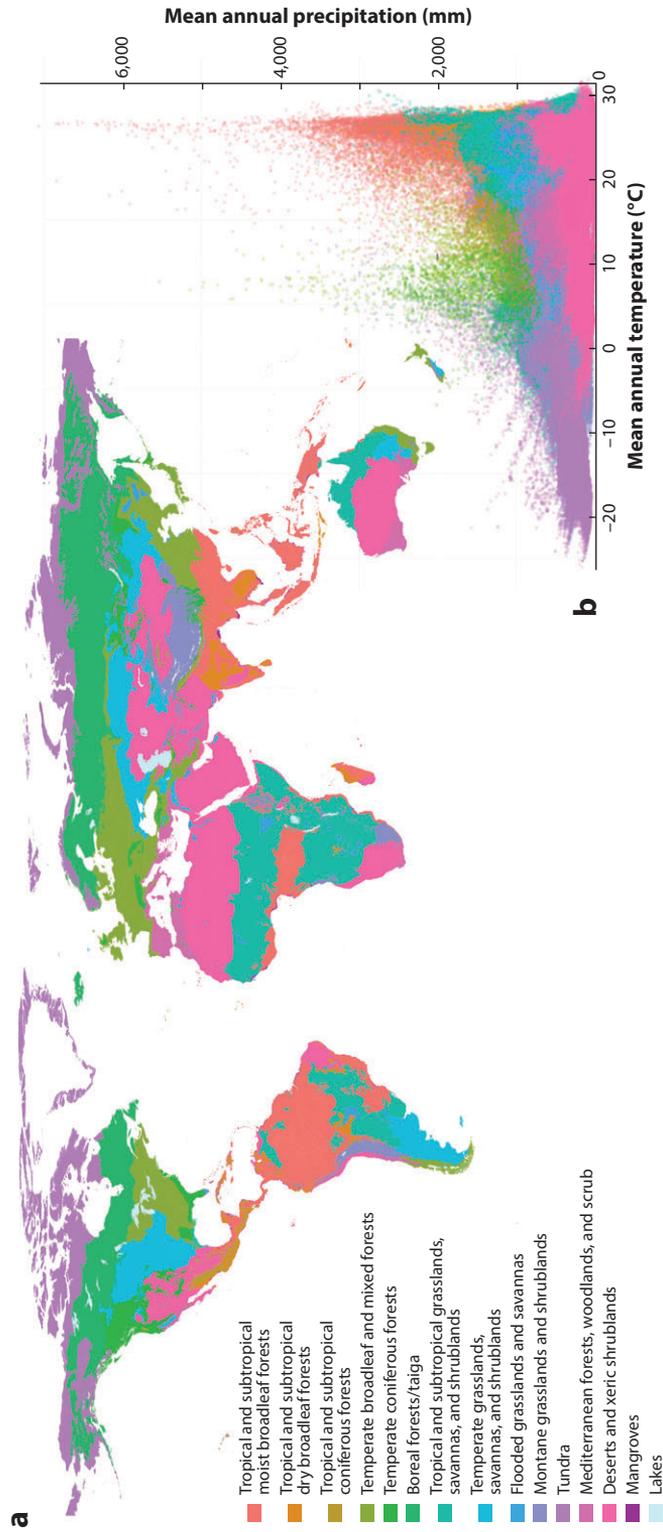
Figure 1

Geography and climate of the world's biomes. (*a*) Map of the World Wildlife Fund "Ecoregions" (**https://worldwildlife.org/publications/terrestrial-ecoregions-of-the-world**; Olson et al. 2001). These regions generally correspond to Whittaker's (1975) original biome types but are slightly broader; although they are suboptimal for some biological purposes (e.g., Särkinen 2011; Hughes et al. 2013) and in need of refinement, they provide a globally manageable number of categories for present purposes. (*b*) The same biomes in relation to mean annual temperature and precipitation estimated from WorldClim climate layers (Hijmans et al. 2005). The relationships depicted by Whittaker (1975) are broadly evident but with substantial climate overlap among biomes.

relevant, we discuss these only to a limited extent, mainly to suggest how they might be integrated into the research program that we envision.

BACKGROUND

What Is a Biome?

The biome problem is similar to the species problem. Different biomes are generally easy to distinguish—for example, tropical rainforest is distinct from Arctic tundra. Yet, it has been difficult to define the biome category itself. From key early treatments (e.g., Schimper 1903), through Whittaker's (1975) seminal work, to the present (e.g., Woodward et al. 2004), biome definitions have variously integrated climate variables (e.g., temperature and precipitation), vegetation structure (e.g., closed forest versus open heathland), and/or the presence of key lineages (e.g., conifers in forests, grasses in savannas) (**Figure 1**). As in the species problem, however, these criteria don't always coincide. For present purposes it is important to appreciate that a choice of any particular biome classification can influence the conclusions: A course-grained set of biome categories will tend to estimate a lower frequency of shifts than a fine-grained set.

Why bother with biomes at all? First, understanding biome shifts can help us piece together the assembly of biotas through time and thereby understand the genesis of a conspicuous structural characteristic of the biosphere. Second, biome shifts are widely viewed as major transitions entailing significant morphological and physiological adaptation. This might often be the case, but not always. Lineages can shift biomes without much evolutionary change (e.g., Ackerly 2004), and profound change can take place within a biome (e.g., Edwards & Donoghue 2006). In any case, focusing on biome shifts gives us a place to begin to explore such issues at a scale that can potentially inform not only our understanding of organismal evolution but also of ecosystem structure, function, and change.

Biomes are distinct from biogeographic "realms" [e.g., the six of Wallace (1876), or the 11 of Holt et al. (2013); see also Kreft & Jetz (2013)] or from floristic kingdoms, regions, and provinces (e.g., Takhtajan 1986). These are not intended to correspond to climatic conditions but instead are meant to represent shared biogeographic history owing to the past existence of isolated centers of diversification for multiple groups of organisms. Realms matter here because they provide an important context within which biome assembly has taken place. They determine which lineages have been available for the occupancy of new environments as these have come into existence. Deserts of the New World, for example, are characterized by the presence of Cactaceae; these are missing and effectively replaced by other lineages in the Old World (e.g., stem succulent Euphorbiaceae in Africa). As we explore below, the numbers, sizes, and adjacencies of biomes within realms are critical to understanding biome shifts.

What Is a Niche?

Various concepts of niche are in use, and this can complicate comparative work. Whittaker et al. (1973, pg. 335) distinguished between "niche" [the ecological role of a species within a community; emphasized by Elton (1927)] and "habitat" [abiotic variables delineating the distribution of a species; often credited to Grinnell (1917); but see Schoener (1989)], and promoted the use of a third term, "ecotope," to summarize "the full range of adaptations to external factors of both niche and habitat." The macroevolutionary studies we review here most often include only climate data, typically obtained from collection localities sampled from the geographic ranges of species. Holt (2009) referred to these as "statistical niche models" and highlighted their promise but also

their limitations, especially as they relate only to the realized habitat. Implicit in this focus is the assumption that physiological tolerances are more important in establishing species ranges than biotic interactions. We return to this issue below in the section titled Integrating Biotic Interactions.

The notion of niche conservatism can be traced to Darwin and has surfaced occasionally ever since (e.g., Good's Theory of Tolerance noted above). The basic idea is that as speciation proceeds, descendant species are likely to retain more or less the same niches as their ancestors, such that closely related species will be ecologically similar. Losos (2008) proposed that "phylogenetic niche conservatism" be invoked only when species are more similar in their niche characteristics than expected based on their relatedness. For Losos, in other words, niche conservatism requires a demonstration that something is positively constraining niche evolution. Wiens (2008) and Wiens et al. (2010) responded to this reasoning, discussed various tests and their limitations, and argued that niche conservatism is both common and highly significant for ecology and evolution.

We note that population biologists tend to view niche evolution as commonplace, whereas comparative biologists often accept niche conservation as the general rule. There are several possible explanations for this contrast (Futuyma 2010), but we think that the use of "niche" has been a key factor (Edwards & Donoghue 2013). Macroevolutionists and macroecologists, for practical reasons, tend to focus only on climatic factors. In contrast, population ecological or microevolutionary studies often include more niche dimensions, with a change along any one of these axes then counting as niche evolution. Both perspectives may be correct, depending largely on scale.

Setting aside practical problems with defining and detecting niche conservatism, we prefer to reorient the discussion around niche evolution, both because it is important in its own right to understanding how lineages have transcended significant ecological boundaries and because this may help explain why other lineages have not. At the level of biomes we can ask whether some transitions are more common than others, and how this varies among lineages and realms. We can also consider what particular factors—intrinsic or extrinsic—increase or decrease the probability of biome shifts of various sorts.

A SNAPSHOT OF THE LITERATURE

The literature on biome shifts in plants is widely scattered and highly uneven—some shifts have received considerable attention (e.g., tropical forests to savannas) and some very little (e.g., temperate to boreal forests). To give the flavor of this research, here we briefly summarize a selection of phylogenetic papers that have focused specifically on biome shifts, several analyses that synthesize a number of phylogenetic studies, and a global strategy using single large phylogenies.

Studies of Individual Clades

The studies discussed below, along with additional cases, are listed in **Table 1**, which also summarizes the different types of data and analyses used. These studies provide a basis for the generalizations developed below.

Shifts into temperate forests. Although it has long been recognized that shifts from tropical forests into the temperate zone must have been common (e.g., Judd et al. 1994) and that temperate clades are often nested within and are younger than tropical lineages (e.g., Kerkhoff et al. 2014), surprisingly few detailed analyses have focused on this shift. One example is *Viburnum* (Adoxaceae), in which recent studies imply with increasing certainty that there were as many as ten shifts from

Table 1   Thirty representative phylogenetic studies documenting evolutionary biome shifts in plants[a]

Study	Lineage	Biome shift	Dated phylogeny	>50% sample	Climate data	Trait data	Biogeography
Smith & Donoghue 2010	*Lonicera*	Temperate mesic/ mediterranean	✓	✓	✓	✓	✓
R.M. Ogburn & E.J. Edwards, in review	Montiaceae	Xeric/montane	✓	✓	✓	✓	–
Töpel et al. 2012	Rosaceae	Multiple	✓	✓	✓	–	✓
Koecke et al. 2013	*Cedrela*	Tropical mesic/ tropical dry	✓	✓	✓	–	–
Crisp et al. 2010	*Livistona*	Tropical mesic/ tropical shrubland	✓	✓	–	–	✓
Salvo et al. 2010	*Ruta*	Temperate mesic/ mediterranean	✓	✓	–	–	✓
Holstein & Renner 2011	*Coccinia*	Multiple	✓	✓	✓	–	–
Arrigo et al. 2013	*Selaginella*	Multiple	✓	✓	✓	–	–
Jara-Arancio et al. 2013	*Leucocoryne*	Mediterranean/xeric	✓	✓	✓	–	–
Schnitzler et al. 2012	*Babiana*	Karoo/Fynbos	✓	✓	✓	–	–
Evans et al. 2009	*Oenothera*	Temperate grassland/xeric	✓	✓	✓	–	–
Schrire et al. 2009	Indigofereae	Multiple	✓	–	✓	–	✓
Heibl & Renner 2012	*Oxalis*	Multiple	✓	–	✓	–	✓
Schmerler et al. 2012	*Viburnum*	Tropical mesic/ temperate forest	–	✓	✓	✓	–
Ireland et al. 2010	*Ateleia*	Tropical dry/ tropical mesic	✓	✓	–	–	–
De-Nova et al. 2012	Bursera	Multiple	✓	✓	–	–	–
Pitterman et al. 2012	Cupressaceae	Temperate conifer/ xeric	✓	–	–	✓	–
Davis et al. 2002	*Acridocarpus*	Tropical mesic/ xeric	✓	–	–	–	✓
Bouchenak-Khelladi et al. 2010	Mimosoideae	Tropical mesic/ savanna	✓	–	–	–	✓
Lohmann et al. 2013	Bignonieae	Tropical mesic/ savanna	✓	–	–	–	✓
Hoffmann et al. 2010	*Ranunculus*	Boreal/tundra (Arctic)	✓	–	–	✓	–
Tkach et al. 2007, 2008	*Artemesia*	Boreal/tundra (Arctic)	✓	–	–	✓	–

(*Continued*)

Table 1 (Continued)

Study	Lineage	Biome shift	Dated phylogeny	>50% sample	Climate data	Trait data	Biogeography
Hörandl & Emadzade 2011	*Ranunculus*	Wetland/montane	✓	–	–	–	✓
Jordan et al. 2005	Proteaceae	Multiple	–	–	✓	✓	–
Edwards & Smith 2010	Poaceae	Tropical mesic/ savanna	–	–	✓	✓	–
Osborne & Freckleton 2009	Poaceae	Multiple	–	–	✓	✓	–
Crayn et al. 2006	Eleocarpaceae	Tropical mesic/ xeric	✓	–	–	–	–
Pennington et al. 2004	*Ruprechtia*	Tropical dry/ tropical mesic	✓	–	–	–	–
Burke et al. 2010	Polygonaceae	Tropical mesic/ xeric	–	–	–	✓	–
Douglas & Manos 2007	Nyctaginaceae	Tropical mesic/ xeric	–	–	–	✓	–

[a]All studies included a phylogenetic tree, and most included a dated tree, but less than half included more than 50% of the species in the focal clade, and fewer included detailed climate data, relevant functional traits, or quantitative biogeographic analyses. These biome shifts are depicted in **Figure 3**. Symbols: ✓, the study includes this type of information; –, study does not include this type of information.

tropical into temperate forests in eastern Asia, as well as shifts from cold temperate into warmer evergreen forests in Asia and into cloud forests in Latin America. Schmerler et al. (2012) showed that these shifts were accompanied by changes in leafing habit, leaf shape, and leaf margins that mirror the global pattern used by paleobotanists to infer past climates. A number of shifts have also been documented from tropical forests into higher elevation cloud forests and even into páramo vegetation, especially in South America (e.g., multiple times within Melastomeae; Michelangeli et al. 2013).

Shifts into dry forests. Pittermann et al. (2012) analyzed several shifts within Cupressaceae from an ancestrally warm, mesic environment (e.g., *Taxodium* in swamps) into more arid zones (e.g., *Cupressus* in deserts). Such shifts occurred independently in the Northern and Southern Hemispheres, in both cases within a lineage characterized by reduced evergreen leaves. Their physiological studies demonstrated the evolution of cavitation-resistant xylem in lineages that radiated into post-Eocene arid environments. Pittermann et al. argued that this came at the cost of increased investment in xylem and reduced photosynthetic rates, which are linked with slower growth rates and smaller stature.

Crayn et al. (2006) showed that the former Tremendraceae, a group of about 50 species of shrubby, dry-adapted Australian plants with generally small, stiff leaves, are nested well within the Elaeocarpaceae, a group of some 500 species, most of which are trees and shrubs of tropical rainforests. This provides a clear example of a shift from tropical forest into arid environments. Although mesic forests were widespread in the Eocene when the Tremandraceae originated, some sclerophyllous plants are documented at that time from Western Australia, where they may have evolved first in response to oligotrophic soils before the spread of drought during the Miocene. Within Tremendraceae, leafless *Tetratheca* seem to have radiated with the onset of Miocene aridification.

Shifts into sclerophyllous shrublands. Salvo et al. (2010) argued that the shift to sclerophyllous leaves in *Ruta* (Rutaceae) in Europe predated the evolution of arid climates around the Mediterranean Basin. *Ruta* appears to have originated earlier to the north and then to have moved into its more southern range before the onset of aridity (which they placed at 9–8 Mya) and the development of the Mediterranean climate (3–2 Mya) that the modern species inhabit. This may be an example of in situ evolution, possibly in parallel in several lineages, in response to gradual change from a subtropical to a Mediterranean climate (see below, the section titled The Problem of Inferring Past Biomes). In contrast, in *Lonicera* (Caprifoliaceae) there appear to have been parallel adaptations (e.g., evergreen leaves) to a Mediterranean climate in southwestern North America and in the Mediterranean Basin at times that coincide with the inferred ages for these climates (Smith & Donoghue 2010). In other cases, seasonally dry tropical forests appear to have been the source of lineages occupying xerophytic scrubland. Ackerly (2004) postulated such an origin for several prominent lineages in the California chaparral, and De-Nova et al. (2012) document nine shifts of this sort within *Bursera* alone.

Shifts into savannas. In Indigofereae (Fabaceae), Schrire et al. (2009) suggested that smaller biomes, or those with harsh climates and/or edaphic conditions, receive relatively fewer immigrants, which then diversify rapidly. Consequently, Indigofereae in succulent and temperate biomes harbor a few diverse clades, as compared with tropical savanna communities, which are larger in size and received more independent lineages. Overall, Schrire et al. (2009), building on the seminal work of Lavin et al. (2004), noted a high level of diversification within biomes in legumes (e.g., *Inga*; Richardson et al. 2001), often spanning geographic realms (e.g., in *Astragalus* there may have been more switches between continents than between biomes; Scherson et al. 2008). However, some groups, such as *Indigofera* and *Acacia*, appear to have shifted readily among certain biomes, especially into tropical grasslands (Bouchenak-Khelladi et al. 2010).

Grasses (Poaceae) using the C4 photosynthetic pathway are a key component of warm grassland biomes. Edwards & Smith (2010) concluded that multiple origins of C4 were consistently associated with shifts into warm, dry areas; climate data support a transition from warm tropical forests into savanna-type ecosystems. These shifts mostly coincided with the Miocene development of extensive grassy and arid biomes, which promoted multiple radiations of grasses and succulent lineages (Bouchenak-Khelladi et al. 2009, Arakaki et al. 2011, Spriggs et al. 2014).

Shifts into arid biomes. Most species of the lycophyte clade *Selaginella* are found today in rainforests, with adaptations to drought arising at least three times independently. Arrigo et al. (2013) showed that one of these shifts from mesic environments accompanied the origin of *Tetragonostachys*, a clade of about 45 species of moss-like xerophytes. These are mainly confined today to arid habitats in southwestern North America, and their dating analyses are consistent with fossil evidence of drying during the middle Eocene. From the arid southwest they document a shift northward into colder, but still dry, climates. They postulated that the evolution of desiccation tolerance facilitated evolution into boreal climates.

In an analysis of *Oxalis* (Oxalidaceae) in Chile, Heibl & Renner (2012) inferred two independent shifts into the Atacama desert from forests and shrublands, more or less coincident with increasing aridity beginning in the mid-Miocene. They suggest that these shifts were enabled by preexisting adaptations to drought, such as root tubers and fleshy leaf bases. Similarly, they inferred six to eight shifts into alpine habitats within arid adapted clades.

Shifts into alpine and Arctic zones. Hörandl & Emadzade (2011) demonstrated multiple shifts of *Ranunculus* (Ranunculaceae) into alpine habitats in mountain systems around the world. They

indicated within-region shifts from lower elevations in the Alps, in the Irano-Turanian region, and possibly in North America, but favored connections involving northern Asia to explain some links between North America and the Himalayas and long distance dispersal events to the Andes, eastern Africa, and New Zealand. They suggested that the occurrence of *Ranunculus* in wet habitats at lower elevations fostered shifts into alpine environments. Hoffmann et al. (2010) showed that there were at least seven shifts within *Ranunculus* into the Arctic zone at various times since the Miocene, again mainly within lineages already adapted to wetland conditions. Unexpectedly, lineages from alpine habitats in mountains to the south were seldom the source of Arctic lineages.

Synthetic Analyses

A number of studies have analyzed sets of phylogenies for plants within a region [e.g., Byrne et al. (2008, 2011), Crisp et al. (2004), and Crisp & Cook (2013) for Australia; Ackerly (2004) for California chaparral; Olmstead (2012) for South America; Guerrero et al. (2013) for the Atacama desert; and Jansson et al. (2013) for tropical-temperate shifts]. Here we highlight three recent examples to illustrate the questions being addressed on different scales.

Crisp et al. (2009) inferred biome shifts for 45 plant clades distributed around the Southern Hemisphere and found that 396 out of about 11,000 divergences (<4%) were associated with biome shifts. Most of these shifts were within landmasses, but 40 accompanied transoceanic dispersal events. They recorded the largest number of shifts out of the sclerophyll biome and into the arid biome. Some shifts were entirely missing, such as between grasslands and bogs, bogs and arid areas, and savanna and alpine. They noted that older biomes (e.g., sclerophyll) tended to serve as sources and younger ones (e.g., arid, alpine, grassland) as recipients.

Comparing stem-node ages for biome-endemic lineages across 17 plant clades, Verboom et al. (2009) attempted to date the Fynbos and succulent Karoo biomes of the Greater Cape flora of southern Africa. They found that succulent Karoo lineages were mostly less than 10 Ma old. In contrast, Fynbos lineages showed a wider range of dates, some back to the Oligocene. In individual clades with representatives in both biomes, they mostly inferred shifts from Fynbos to succulent Karoo (except *Babiana*; cf. Schnitzler et al. 2012). They concluded that succulent Karoo originated more recently with increased aridification in the Miocene; the older Fynbos provided a refuge for more ancient elements, including Restionaceae and Bruniaceae.

Simon et al. (2009) analyzed four plant clades to reconstruct the recent assembly of the fire-prone savanna biome in South America (for a comparable study in Africa, see Maurin et al. 2014 and Pennington & Hughes 2014). These contained 15 cerrado lineages (11 in *Mimosa*) that originated within the past 10 Ma (mostly the past 4 Ma), mainly from wet and seasonally dry forests. Several shifts also occurred from cerrado back into forest habitats. In Verbenaceae, Olmstead (2012) highlighted a shift into cerrado from wet forests in *Stachytarpheta*, but also from arid-adapted ancestors in *Lantana/Lippia*. These observations, combined with plastic responses in fire traits within species, and the wide variety of adaptations to fire (thick corky bark, xylopodia, pachycauly, apically clustered leaves and stipules), suggest that fire has not posed a strong barrier to biome shifting in woody plants.

Global Analyses

An emerging approach combines information from various preexisting databases to analyze large numbers of shifts in a single global analysis. For example, Smith & Beaulieu (2009) combined a large angiosperm phylogeny with growth form and climate data to infer rates of climate niche evolution in woody versus herbaceous species and concluded that woody species show higher levels of niche conservatism. Zanne et al. (2014) used a similar data set and included additional variables

such as leafing habit and wood anatomy for a subset of their study species. They concluded that movements into and out of freezing environments have been frequent and that transitions into areas experiencing freezing temperatures were most common within lineages of evergreen plants or those which had already evolved small vessel diameters or the herbaceous habit.

A CONCEPTUAL FRAMEWORK

To better orient the research described above, and specifically to begin to specify a set of null expectations, we continue the development here of a general conceptual framework, building primarily on ideas by Donoghue (2008) and Edwards & Donoghue (2013). This relates the probability of niche evolution to the evolutionary accessibility of adaptations within lineages and to their exposure to new environments over time. Although we focus here on plants and on biome shifts, we believe that this framework accommodates niche shifts more generally and will also aid in understanding spatial and temporal biodiversity gradients.

Donoghue (2008) contrasted the likelihood of movement via habitat tracking into similar environments in separate regions with the likelihood of evolving adaptations to newly originating environments. Edwards & Donoghue (2013) added to this the varying likelihood in different clades of evolving relevant adaptations. The idea is that some lineages appear to be predisposed to making certain transitions, as evidenced by the clustering of such changes in phylogenetic trees (e.g., 22–24 origins of C4 photosynthesis within a single clade of grasses; see above). Whether it is easier to move or to evolve depends both on the presence of lineages that can readily adapt to the novel conditions and on the spatial configuration and biodiversity of the contrasting environments (see Edwards & Donoghue 2013, their figure 1).

Here we extend this line of thinking with the help of **Figure 2**, which shifts the focus away from dispersal into a new biome and toward in situ responses to the onset of a new climatic regime. Specifically, in **Figure 2a** we imagine a new climate moving as a front across a landscape. We focus on this simple case while acknowledging that there will likely be spatial and temporal heterogeneity in the process, as shown in **Figure 2b**. The species that directly encounter the advancing front (belonging to lineages A–D) have the opportunity to adapt to the new conditions. An extreme case of niche conservatism is shown in **Figure 2c**; none of the existing lineages are able to adapt to the new climate, and they either migrate or go extinct. The other extreme—complete niche lability—is represented in **Figure 2d**, where all the lineages have managed to adapt in situ to the new climate. Most real cases presumably lie in between, with some lineages transcending the boundary and others not, as in **Figure 2e**. Of course, it is possible that a given species might migrate *and* evolve in situ, potentially resulting in ecological speciation (A$_1$ in **Figure 2e**). Adaptation to a new biome may or may not also influence the subsequent rate of diversification (Sauquet et al. 2009, Valente et al. 2010, Koenen et al. 2013).

We now can add various complexities. All else being equal, more lineages are expected to adapt to the new climate where there are more encounters with it and vice versa. In **Figure 2f**, we insert a barrier (say, an ocean) to create two biome and boundary sizes. The number of lineages that transcend the boundary should at least partially scale with the absolute size of each environment and with the boundary length. The dimensions of the boundary zone—its length, width, and even topographic complexity—may be especially critical, as this is the arena in which adaptive divergence is likely to be initiated.

We can extend this line of thinking and imagine two biomes that never come into direct contact with one another. Long-distance dispersal would then be required to bridge the gap, presumably decreasing the probability of a successful shift. The likelihood of shifting between
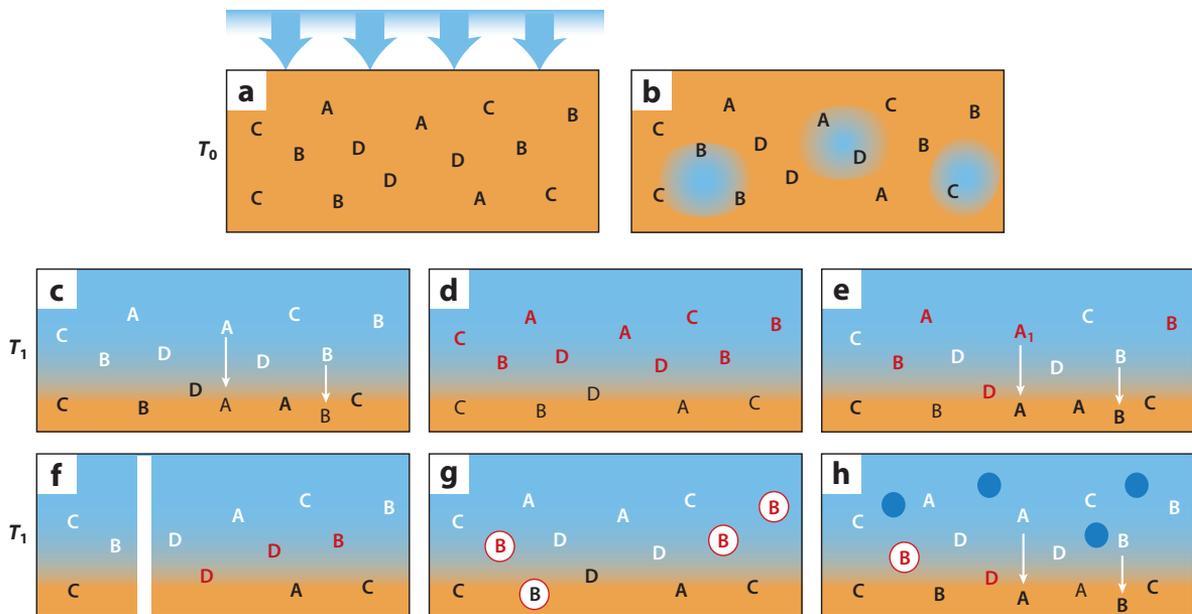
Figure 2

Climate change, niche evolution, and the assembly of a new biome. At T_0 an ecological community occupies the homogeneous environment in orange. Letters A–D represent species belonging to four distinct clades. Climate change moves (*a*) as a front across the landscape or (*b*) as patches within the ancestral environment. At T_1 the blue environment is established adjacent to the reduced orange environment; a transitional zone remains along the boundary. (*c*) Complete "niche conservatism" (*white-lettered species* failed to adapt; *arrows* indicate migration). (*d*) Complete "niche evolution" (*red-lettered species* adapted in situ). (*e*) Combination of panels *c* and *d*—some species adapt, some migrate, some go extinct, and some may adapt and migrate, resulting in ecological speciation (A_1). (*f*) The white line separates two geographically distinct zones of biome adjacency. P_g increases with the size of the boundary separating the two biomes, as boundary transitional areas may be an especially active area of biome shifting. (*g*) P_o is higher in lineage B with an "enabling" trait, indicated by the white circles. (*h*) P_b is decreased by the presence of lineages already well adapted to the blue climate (*blue circles*). P_g = probability that a lineage will shift into a new biome due to geographic opportunity; P_o = probability that a lineage will shift into a new biome due to intrinsic proclivity of a lineage to evolve along a particular climate axis; P_b = probability that a lineage will shift into a new biome due to both positive and negative ecological interactions.

two biomes should scale with the distance separating them, though this could be offset by their relative environmental similarity and/or the dispersal abilities of the organisms involved.

We can also attach different probabilities of adapting to the new environment to members of the different clades, as shown in **Figure 2g**. Let's suppose that members of clade B are far more likely to adapt to the emerging biome than are members of the other clades, owing perhaps to some precursor enabling state (Marazzi et al. 2012, Christin et al. 2013) or to a background rate of change in a character that facilitates the shift (Beaulieu et al. 2013; R.M. Ogburn & E.J. Edwards, in review). In any case, members of clade B adapt readily and multiple times to the new environment, whereas other lineages are slower to make the shift.

To this model we can also add the effects (positive or negative) of organisms that are already adapted to the spreading environment, having perhaps tracked it from elsewhere (**Figure 2h**, *dark blue circles*). These migrating lineages might outcompete less well-adapted populations, thus limiting successful establishment. However, they could also facilitate transitions, either by changing the physical environment (e.g., nurse plants) or via interacting species (e.g., pollinators or herbivores) that could potentially advantage newly evolving populations. This thinking extends not just

to individual species or to species richness, but also to the phylogenetic and functional diversity of the source and receiving zones (e.g., Strauss et al. 2006, Davies et al. 2010).

The ideas represented in **Figure 2** can be boiled down to a simple equation:

$$P_{\text{shift}} = P_{\text{g}} \times P_{\text{o}} \times P_{\text{b}},$$

where P_{shift} is the probability that a lineage will shift into a new biome, calculated as the joint probability of three factors: P_{g}, which represents the relative geographic opportunity for movement; P_{o}, which is the intrinsic proclivity of the lineage to evolve along a particular climate axis; and P_{b}, which includes both positive and negative ecological interactions with the species already occupying a new environment.

Time is a final critical dimension. P_{shift} is an instantaneous measure, for any given moment in time, but P_{g}, P_{o}, and P_{b} are highly dynamic and will change through time in complex and potentially opposing ways. For example, we imagine that for a lineage living in a tropical forest, P_{g} for adapting to the temperate zone has decreased significantly over the past 30 million years, as the length of the shared boundary between these two biomes has declined (see below, hypotheses 2 and 3 in the section titled Emerging Patterns and Hypotheses). P_{b} is likely also to have declined, as the diversity of organisms occupying the temperate zone increases and niche space fills. P_{o} will vary with potentially enabling traits that are gained or lost, and also with the rate of lineage diversification—all things being equal, a more diverse lineage will present a greater number of species with an opportunity for shifting, and the stochastic element of biome shifting will favor more shifts within diverse groups. Given enough time, we imagine that any two-biome system could come to resemble the highly labile scenario portrayed in **Figure 2d**; the imbalances we see today may largely reflect the highly dynamic nature of Earth's climate and geology.

EMERGING PATTERNS AND HYPOTHESES

Oriented by this conceptual framework, here we initiate a synthesis around a series of interrelated (and not mutually exclusive) hypotheses on the probability of biome shifts (P_{shift}). The first three hypotheses concern largely abiotic factors (P_{g}), whereas the last three refer to biotic factors (P_{o} and P_{b}). Several of these hypotheses have considerable support already; others are far more speculative.

Hypothesis 1. P_{shift} Depends on Biome Size

Figure 3 displays modern biome sizes within the global temperature and precipitation space. Deserts and xeric shrublands (here including both warm and cold deserts) are the most extensive, with tropical dry forests and Mediterranean woodlands at the other end of the spectrum. We might expect many biome shifts into and out of the larger biomes and fewer involving the smaller ones. The literature lends support to this argument, with multiple studies showing biome shifts out of tropical forests into drier and colder biomes, and many shifts into the extensive shrublands, grasslands, and deserts. It is clear, however, that size alone does not fully explain the frequency of shifts; for example, there are few documented shifts involving widespread temperate grasslands and boreal forests.

The influence of biome size on P_{shift} may largely be a function of the relative biodiversity of source and recipient biomes. Specifically, we might expect successful shifts to be more likely from source biomes that contain more lineages than from those with lower diversity. It may be possible to disentangle these effects as size and biodiversity are not perfectly correlated. For example, it appears that hyperdiverse moist tropical forests are involved in more biome shifts (serving especially as a source) as compared with the also widespread but less diverse boreal forests. This thinking can extend to differences in biome diversity in different realms. For example, there may
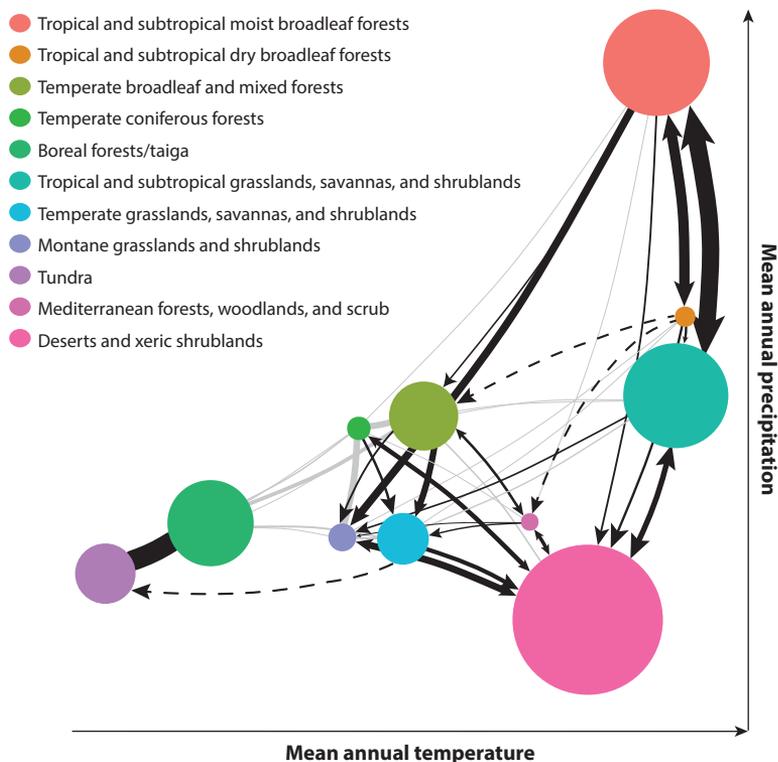
Figure 3

Sizes and connections of modern biomes. Biome categories correspond to **Figure 1**. Circle sizes reflect the total global area occupied by different biomes; these are centered on the average mean annual temperature and mean annual precipitation for each biome. Connecting lines represent existing boundaries between pairs of biomes; line thickness corresponds to the total length of shared perimeter, with the exception of the thinnest line, which represents a range of lengths between 131–3,586 km. Evolutionary biome shifts reviewed here are shown in black; others are in gray. Arrows indicate inferred directions of shifts.

have been more shifts into savannas from the more diverse rainforests in South America than there were from the less diverse tropical forests in Africa (but see recent analyses by Maurin et al. 2014 and Pennington & Hughes 2014). The same may be true of the diverse temperate forests of eastern Asia in relation to shifts into boreal, grassland, and alpine biomes.

Hypothesis 2. P_{shift} Depends on the Spatial Adjacency and the Boundary Between Biomes

Figure 3 shows the lengths of the boundaries between every pair of biomes as these are presently distributed. The expectation is that more shifts will take place between adjacent and broadly connected biomes than between those that are geographically disjunct or narrowly connected. The literature strongly supports this hypothesis. We know of no examples of shifts between the most widely separated biomes, such as between tropical forests and tundra. Instead, almost all the documented shifts are between directly connected biomes. For example, nearly all the shifts of woody plants into savanna systems have been from adjacent wet and dry tropical forests rather than, for example, from temperate or boreal forests. The effects of geographic continuity can be more subtle, such as in the biased origination of mangroves from terrestrial ancestors in the Old

World tropics versus the New World, which Ricklefs et al. (2006) attributed to the existence of more small islands in shallow seas in the Indo-West Pacific region.

We think that at least three factors underlie this pattern. First, adjacency provides geographic opportunity, and the longer the border between two biomes the greater the likelihood that lineages will adapt to the new environment. Second, adjacent biomes are often climatically similar to one another, providing a natural "path of least resistance" to move into new ecological zones. Third, adjacent areas are most likely to have been subjected to the gradual climate change depicted in **Figure 3**, in which lineages adapt in situ. This type of change may provide time for selection to act within the boundary zone on well-established populations only mildly maladapted to the novel climate.

Hypothesis 3. Biome Shifts Depend on Biome Ages and Connections Through Time

Figure 3 shows the modern distribution of biome types, but their sizes and connectivities have changed considerably through time. For example, tropical forests were much more broadly distributed in the Eocene and were more extensively connected to temperate forests (Fine & Ree 2006). The number of biome shifts that have taken place may best be predicted by taking into account the sizes and connections of biomes in the past, as opposed to just the current configuration. A time-integrated approach (cf. Fine & Ree 2006, Jetz & Fine 2012) would be ideal in this case, but the past distribution of biomes remains a matter of considerable speculation (see below, the section titled The Problem of Inferring Past Biomes), and at this stage quantitative measures of size and connectivity would be highly imprecise if not positively misleading. Changes through time are likely reflected in an excess of certain transitions above what would be predicted by modern sizes and connections. For example, many more transitions are suspected between tropical and temperate forests than one would predict solely on the basis of the limited modern connection between these biomes in eastern Asia. Instead, the number of shifts probably better reflects the greater continuity of tropical and temperate systems in Asia as compared with the New World (Latham & Ricklefs 1993, Qian & Ricklefs 2000, Donoghue 2008).

Knowledge of temporal changes in biome dimensions may be especially critical in explaining asymmetries in the direction of biome shifts. In general, older and once more extensive biomes (e.g., tropical rainforests) tend to be donors, whereas younger and once less extensive biomes (e.g., deserts, Mediterranean scrublands, alpine and Arctic habitats) tend to be recipients. Tropical rainforests provide a case in point. Although they have served as the source for many lineages now occupying other biomes, we have little evidence in plants of shifts into rainforests. Why might this be? Setting aside sampling bias, the ancient development of tropical rainforests (Burnham & Johnson 2004)—either somewhat before or not long after the Cretaceous-Paleocene boundary—makes it difficult to confidently infer source areas for the originally colonizing lineages. A case has been made in legumes (Fabaceae) that there were multiple shifts into moist tropical forests, both northward and southward, from a seasonally dry forest biome that may have occupied a global belt through the Tethys Seaway as early as the Paleocene (Lewis et al. 2005). After the initial spread of rainforests, the movement of plant lineages into them appears to have been rather limited and mainly from adjacent tropical biomes [often reentry from dry forests or savannas; e.g., Bignonieae (Lohmann et al. 2013); *Ruprechtia* (Pennington et al. 2004); *Ateleia* (Ireland et al. 2010); *Bursera* (De-Nova et al. 2012)]. The rarity of inferred temperate to tropical transitions in plants could reflect differences in the extent of these two biomes in the past, tropical forests being more widespread and temperate forests less so. However, as we note below (in the section titled Integrating Biotic Interactions), biotic factors have also been implicated in explaining this asymmetry.
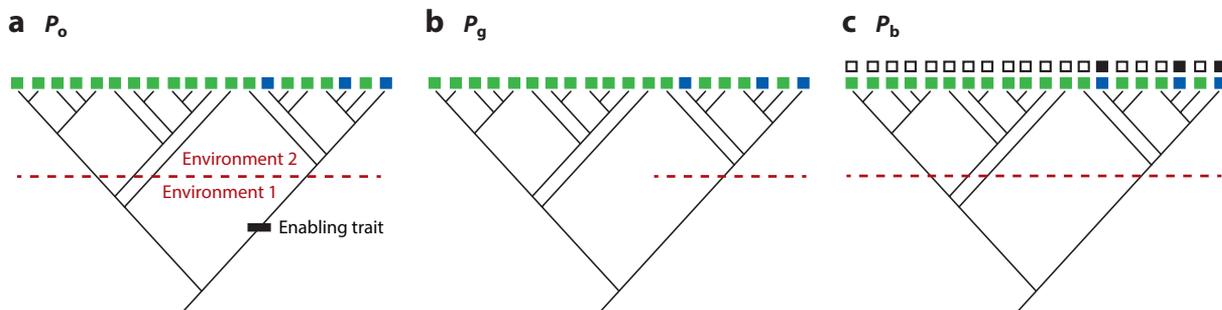
Figure 4

Phylogenetic clustering of biome shifts in relation to P_g, P_o, and P_b. Most species in this hypothetical lineage occupy the "green" biome; multiple shifts to the "blue" biome in one subclade indicate a higher P_{shift}. This could be due to (*a*) P_o, all species are exposed to environment 2, and an enabling trait facilitates adaptation to the blue biome; (*b*) P_g, the entire clade is "enabled," but only one subclade is exposed to the new environment; (*c*) P_b, the entire clade is exposed, and the subclade is "enabled," but shifts into the blue biome occur only when a particular lineage (*black squares*) is present in the new environment. P_g = probability that a lineage will shift into a new biome due to geographic opportunity; P_o = probability that a lineage will shift into a new biome due to intrinsic proclivity of a lineage to evolve along a particular climate axis; P_b = probability that a lineage will shift into a new biome due to both positive and negative ecological interactions.

Hypothesis 4. Biome Shifts Are Highly Clustered in Plant Phylogeny

One of the clearest signals emerging from the literature is that if a lineage has shifted between a pair of biomes, it is likely to have done so multiple times. In nearly every case—be it grasses into savannas or buttercups into alpine zones—studies of particular clades have tended to identify multiple evolutionary shifts between biomes. This suggests an elevated P_{shift} in these groups. As illustrated in **Figure 4**, we often can't determine whether this is due to P_o (e.g., a preexisting enabling trait) or to P_g (e.g., prolonged exposure to a given biome boundary), or even to P_b (e.g., lack of competitors in the new environment). As suggested above, it is likely to be a combination. In the case of grasses, for example, the lineage that repeatedly invaded savannas had both enabling properties (enlarged bundle sheath cells that facilitated the evolution of C4 photosynthesis) and geographical proximity (occupying adjacent tropical forests).

Hypothesis 5. P$_{shift}$ Depends on Preexisting "Enabler" Traits

This hypothesis focuses on just one of the factors mentioned above to explain differences among lineages in the propensity to undergo particular biome shifts. Sclerophyllous leaves provide an example. This leaf type has rarely evolved in direct response to shifts into a Mediterranean biome (but see Smith & Donoghue 2010). Instead, its preexistence in a lineage seems to have facilitated such shifts (Ackerly 2004, Verdú et al. 2003, Jordan et al. 2005, Salvo et al. 2010). Sclerophyllous leaves can mediate several different stressors simultaneously: A long leaf life span promotes high nutrient-use efficiency, a high proportion of cell wall to thicker cell wall permits low leaf-water potentials, and a thick cuticle and an abundance of sclereids minimize excessive radiation loads. The origin of such leaves may have been driven by any one of these factors, preadapting them to cope with the others. Thus, a sclerophyllous leaf that evolved in a high-rainfall, low-nutrient environment (see Crayn et al. 2006) might provide enough drought tolerance for that species to establish in a more arid environment, allowing time for natural selection to fine-tune other aspects of its physiology to accommodate new growth limitations.

Succulent lineages that span arid and forest biomes (e.g., cacti, bromeliads, even *Peperomia*) provide another example of a "gateway" trait—Crassulacean acid metabolism (CAM) photosynthesis in succulent plants preadapts them to life as a tropical forest epiphyte, at least in terms of water relations. In this case, the dramatically different light environments in open arid biomes versus in the subcanopy of a forest spurs subsequent evolution, but CAM may allow a "foot in the door" that effectively buys time for physiological optimization.

Other cases relate to the multiple ways in which plants have adapted to cope with fire (Simon et al. 2009, Keeley et al. 2011). For example, the production of bulbs or tubers for storage could predispose shifts into fire-prone environments. Likewise, the propensity to perennate or to sprout following injury, or flexibility in the periderm production, would facilitate such shifts. Other examples are more subtle, but they are significant in explaining shifts between a particular series of biomes, such as the tendency to thrive in open habitats (e.g., Melastomeae; Michelangeli et al. 2013). Finally, we note that heightened phenotypic plasticity might serve as an enabler; for instance, the tendency for individual species of Bignonieae to occupy both rainforests and cerrado, perhaps owing to their flexibility in switching between shrubs and liana growth forms, could be an enabling trait (Lohmann et al. 2013).

Hypothesis 6. P_{shift} Depends on the "Openness" of Different Communities in Terms of Biotic Interaction

The probability of successful colonization may be greatest when a new environment is first materializing (as in the scenario depicted in **Figure 2**) and perhaps relatively empty, at least along its leading edge (Ackerly 2003). The same reasoning applies to emerging oceanic islands, in which the lack of competition may also promote ecological release and niche shifts (e.g., the Hawaiian silversword alliance; Baldwin & Sanderson 1998). The reverse may also be true. For example, the striking absence of documented shifts from temperate biomes into tropical rainforests (as distinct from shifts into higher elevation forests within tropical latitudes) might mostly reflect P_b resulting from intense competition and predation from densely packed rainforest residents. Such "priority effects" may have significant impacts on the likelihood of shifting (Belyea & Lancaster 1999).

Finally, and somewhat counterintuitively, specialization could promote biome shifting by reducing competition. For example, once angiosperm lineages have evolved into freshwater habitats (probably over 200 times; Cook 1999), they seem able to move easily among such environments across biome and realm boundaries, from the tropics to the poles, seemingly oblivious to major temperature differences. Across most biomes, freshwater habitats are occupied by a very small subset of cosmopolitan aquatic plant lineages (e.g., Alismataceae, Potamogetonaceae, Menyanthaceae, Lemnoideae within Araceae, *Ceratophyllum*). The same argument may hold for some specialized parasitic plants (e.g., Orobanchaceae, Santalaceae).

OVERARCHING ISSUES

Integrating Biogeography and Population Biology

We have adopted the terms shift and shifting (as opposed to "move" and "moving") to remain neutral about whether evolution into a new environment occurred with dispersal or whether it occurred in situ as the environment changed. The easiest cases to sort out are those entailing long-distance dispersal into a disjunct realm (inferred using biogeographic methods with dated phylogenies) combined with independent knowledge of whether particular climates or continental

connections existed at relevant times (e.g., Crisp et al. 2009). We suspect that shifts between adjacent biomes have instead often involved gradual, in situ change within boundary zones (**Figure 2**), but there are intermediate possibilities involving dispersal from nearby areas that are not directly adjoining an advancing front. Also, as suggested by Guerrero et al. (2013) for the hyperarid Atacama desert, there could be substantial lag times in the successful occupancy of extreme environments.

More attention needs to be paid to the interplay between the extent of dispersal between biomes in different biogeographic realms and the ways in which dispersal limitation (combined with priority effects) might isolate some biome types more than others. This line of research, exemplified especially by the work of Lavin et al. (2004) and Pennington et al. (2009, 2010) on seasonally dry tropical forests, should provide insights into geographic opportunities through time (P_g) and the relative importance of habitat tracking.

We suppose that many successful shifts involved a period of repeated colonization, with some degree of plasticity allowing the establishment of individual plants, at least temporarily, thus enabling subsequent evolution (West-Eberhard 2003). Much more attention must be paid to population dynamics, community interactions, and the genetics of colonization and especially to how these interact with the evolutionary opportunities along leading versus trailing edges of species ranges (Ackerly 2003, Gilman et al. 2010). These dynamics could, under some circumstances, also promote hybrid or ecological speciation (Gross & Rieseberg 2005, Schluter 2009).

The rapid mixing of the world's biota by humans provides us with an underexploited real-time experiment in biome shifting. Studies of the rapid adaptation of invasive species to new environmental conditions will provide insights into the roles of environmental stress, standing genetic variation, genetic bottlenecks, and polyploidy in biome shifting (e.g., Saltonstall 2002, Prentis et al. 2008), and we will likewise benefit from analyses of the effects of exotic species on diversification (Vellend et al. 2007). However, it is important to appreciate that there may be significant differences in the factors that govern the establishment of exotic species today and biome shifting in the distant past. For example, the adjacency of biomes (see above) is presumably not as important in the Anthropocene—given the many new means of transporting biodiversity—as it was in preceding eras. Likewise, increased fragmentation of the landscape diminishes options for habitat tracking in the face of environmental change (e.g., Donoghue 2008).

Integrating Biotic Interactions

Attention has mainly focused in this literature on how lineages adapt to changes in abiotic variables (temperature, precipitation, fire, etc.), but biotic interactions could be more significant. For example, as noted above, the paucity of documented shifts in plants from temperate forests into tropical forests may have more to do with competition with well-adapted residents, or to pathogens and herbivores, than it does with physiological adaptation to tropical climates. Data on such biotic interactions are generally much more difficult to obtain than are geographic localities and associated climate data, both of which can now be downloaded without leaving the office. Yet without more ecological detail, we are far from evaluating, to quote Whittaker et al. (1973, p. 334), the "ultimate evolutionary context of a species."

With respect to biome shifts, the nature of competitive interactions along the edges of a species range may be the key to understanding the successful occupation of new biomes (Ackerly 2003). Herbivores could also have a powerful impact on the process (Fine et al. 2013). Significant niche expansion by many invasive species (e.g., Gallagher et al. 2010, Guisan et al. 2014) implies a major disconnect between fundamental and realized niches, due either to dispersal limitation or to the role of competitors, predators, pathogens, and/or facilitators.

The Problem of Inferring Past Biomes

Verboom et al. (2009, p. 45) succinctly stated the logic underlying the inference of past biomes using phylogenetic trees: "...presumably, a lineage endemic to a particular biome did not exist prior to the appearance of that biome." In a number of published studies, independent lines of evidence appear to agree with one another (e.g., Verboom et al. 2009, Becerra 2005), at least roughly, and the conclusions then seem straightforward. However, the precarious nature of such inferences becomes apparent when different lines of evidence conflict.

Consider the conclusion by Davis et al. (2005) that tropical rainforests existed in the mid-Cretaceous. Based on their finding that Malpighiales began diversifying about 110 Mya, and on the fact that modern Malpighiales are dominant elements in the understory of rainforests, they concluded that such forests must have existed at that time. An analysis of the timing of the early radiation of palms (Arecaceae) supported this same conclusion (Couvreur et al. 2011). This reasoning assumes that Malpighiales and Arecaceae retained their presence in rainforests; that is, niche conservatism. This conflicts, however, with the accepted paleontological evidence of the appearance of multistratal rainforests (with lianas, epiphytes, etc.) shortly after the Cretaceous-Paleocene boundary (e.g., Burnham & Johnson 2004, Jaramillo & Cárdenas 2013). Which of these inferences is correct? One possibility is that the fossil record is biased, and another is that the tropical forest understory niche was not conserved but instead evolved in parallel in multiple major lineages of Malpighiales and Arecaceae that presumably existed in the Cretaceous (cf. Crisp & Cook 2012).

The general problem is illustrated in **Figure 5**, which was inspired by the study of *Ruta* by Salvo et al. (2010). *Ruta* are generally sclerophyllous plants that are now endemic to the Mediterranean climate in Europe. A simple explanation would be that sclerophyllous leaves evolved once in the ancestor of this lineage as an adaptation to the Mediterranean climate (**Figure 5a**). Salvo et al. (2010) dated the crown radiation of *Ruta* at ca. 20 Mya, and, in the absence of other information,
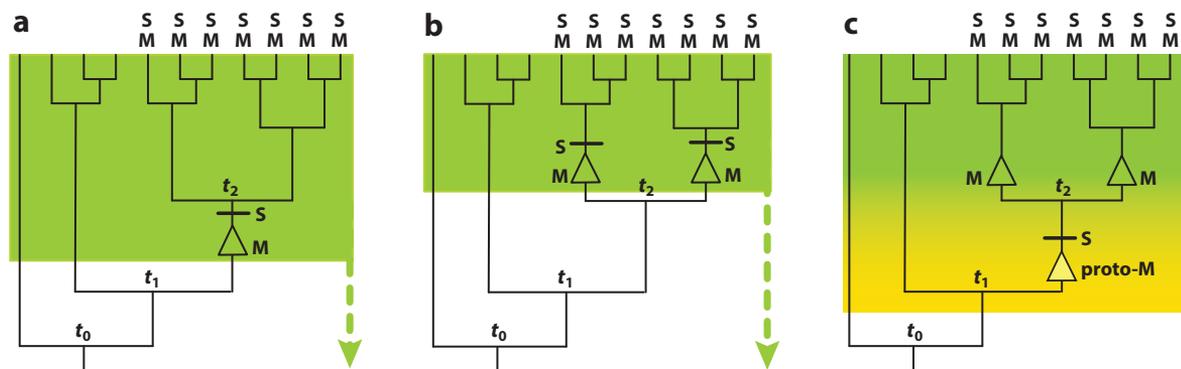
Figure 5

Inferring biome age from a phylogenetic pattern. (*a*) If a lineage is endemic to a given biome (in this case, M, for Mediterranean), it is standard practice to infer (assuming niche conservatism) that the biome came into existence sometime before the radiation of the crown clade at time t_2 (perhaps where shown, as depicted in *green*, or earlier, as indicated by the *green arrow*). If all members of this clade also have sclerophyllous leaves (S), it might be inferred that S evolved once, perhaps as an adaptation to the M climate. (*b*) It is possible, however, that niches are more labile and that there were multiple shifts into the M climate, perhaps accompanied by the independent evolution of S. In this case, the M climate might have emerged after t_2, that is, after the origin of the Mediterranean crown clade. (*c*) Alternatively, S might have evolved in a proto-M climate that emerged earlier (depicted in *yellow*, between t_0 and t_1), possibly with no modern analog (perhaps arid, but with summer rainfall). If so, the presence of S in this lineage might have enabled multiple shifts into the M climate when it emerged.

it might be concluded that the Mediterranean climate existed at that time. However, such a conclusion conflicts with independent evidence that widespread aridification began ca. 10 Mya and that a summer-dry Mediterranean climate originated ca. 3 Mya. There is some possibility that this climate interpretation is incorrect (e.g., see Edwards et al. 2010), but if we accept it at face value, there are several other possible explanations. Shifts into the Mediterranean climate and the evolution of sclerophyllous leaves might have occurred several times independently within *Ruta* (**Figure 5b**), or sclerophyllous leaves might have evolved in the ancestor of *Ruta* in response to something other than summer drought (perhaps in a nonanalog proto-Mediterranean climate), which preadapted them to occupy the Mediterranean climate when it later emerged (**Figure 5c**).

The Davis et al. (2005) and Salvo et al. (2010) studies highlight the possibility of overestimating the age of a biome based on dated phylogenies alone, but underestimation is possible as well, as in the lag-time example of Guerrero et al. (2013) noted previously. As suggested above, the problem may be our reliance on modern biomes when plant assemblages of the past may have no modern analogs. Perhaps Malpighiales radiated in a precursor rainforest setting—in a warm closed-canopy environment similar to, but not perfectly matching, any rainforest today (e.g., Upchurch & Wolfe 1987). If so, this could be an example of an in situ, gradual, massively parallel set of biome shifts (Crisp & Cook 2012).

In general, we need to be more cautious about drawing conclusions only on the basis of dated phylogenies, taking even more seriously the possibility of nonanalog biomes (e.g., Williams & Jackson 2007) and gradual and concerted parallel adaptation (e.g., Cunningham 1999). Beyond this, the detailed analysis of associated functional traits could be useful in choosing among alternative scenarios. A critical assessment of the degree of specialization of a particular functional trait for a particular environment could help to choose between the scenarios depicted in panels *b* and *c* of **Figure 5**. For example, **Figure 5c** might be favored by the knowledge that sclerophyllous leaves are adaptive for arid climates quite broadly and not specifically for summer drought. In the end, the most robust assessments will be those based on multiple phylogenies (incorporating functional traits as well as dates) combined with multiple independent lines of evidence bearing on past environmental conditions.

A Commentary on Alternative Approaches

As the study of biome shifts advances, which approaches are likely to be the most productive? Our conceptual framework and hypotheses highlight the need for detailed knowledge of both clade and environmental contexts. We believe, therefore, that progress is most likely to be achieved by generalizing from multiple case studies of biome shifts within particular clades—studies in which one can assess the distribution of relevant characters, the phylogenetic clustering of events, biogeographic movements, and particularly relevant abiotic and biotic factors. In addition, analyses of individual clades are most likely to benefit from expert evaluation of the completeness of the taxonomic sampling and the confidence in various sources of evidence. We agree with Hughes et al. (2013) about the value of synthesizing general patterns from focused studies of processes within individual biomes.

We are less optimistic about the primary alternative approach, namely global analyses that conjoin very large phylogenies with trait and environmental data to infer, in a single model-fitting exercise, likely evolutionary pathways underlying biome shifts. First, such studies assume the existence of a single model and a set of parameters of character change that govern the evolutionary process across the entire phylogeny or at least across very large clades (e.g., super-rosids, superasterids, monocots, and magnoliids in Zanne et al. 2014). In general, this seems dubious in light of the tendency we have highlighted for character changes to be phylogenetically

clustered. More specifically, Beaulieu et al. (2013) showed for campanulid angiosperms that rates of character change not only vary greatly across the tree but that clade-specific heterogeneity has major consequences for model selection.

Second, given their focus on inferring global evolutionary processes, individual evolutionary events and sequences tend to be backgrounded in such studies. Zanne et al. (2014), for example, cited no specific instances of evolutionary sequences that support (or contradict) their preferred models. This is the opposite of the bottom-up strategy in which individual evolutionary events, set in context, are precisely the data upon which generalizations are based. This, in turn, relates directly to the issue of underlying causation. Our conceptual framework incorporates not just the likelihood of adaptation but also the likelihood that lineages encounter new environments and biotic interactions over time, and each of these factors will vary considerably among lineages. The bottom-up approach facilitates the tracking of particular circumstances at particular times that might influence biome shifts, whereas these potentially critical details are more difficult to monitor in the global approach.

Third, we are struck by the relatively poor sampling, phylogenetic resolution, and clade support in global analyses to date (e.g., Thuiller et al. 2011; C.C. Davis, H. Schaefer, B.R. Ruhfel, M.J. Donoghue, E.J. Edwards, unpublished material, arXiv: 1406.5211). In smaller studies, these issues can be carefully evaluated and possibly addressed in case-specific sensitivity analyses. Furthermore, the intersection of species included in multiple large databases is often disappointing. For example, the Zanne et al. (2014) phylogeny included 31,749 species, which was pruned to just 860 species that were widely scattered across the angiosperms, for their analyses of xylem vessel diameter.

A diversity of approaches, at different spatial and phylogenetic scales, can, of course, yield complimentary insights. Our point is only that the biome shift problem will benefit especially from detailed analyses of individual cases, bringing as much relevant data to bear in well-sampled and confidently resolved clades. Multiple studies of this sort are necessary, we believe, to provide a solid foundation on which to build robust generalizations. One possible value of large "birds-eye" view phylogenetic studies is that they may identify regions in the tree where focused studies of biome shifts might be especially productive.

CONCLUDING REMARKS

Returning to the locomotive analogy with which we began our review, it is clear that the "connecting rod" of plant tolerance is not nearly as rigid as Ronald Good supposed it to be. Recent phylogenetic studies have clearly shown that biome shifts are a regular feature of plant evolution. The challenge now is to identify the factors that regulate major evolutionary changes in tolerance and, ultimately, to explain and predict why some species respond by migrating and others by adapting.

Although we have a long way to go, we are hopeful about the prospects. As we have emphasized, the relative accessibility of adaptations and new environments over time are keys to understanding biome shifts. With enough carefully conducted case studies that integrate disparate data sources and analyses and that are designed to specifically test the hypotheses highlighted above, we are confident that many of the findings reviewed here will be supported, but also that many new insights will emerge. As in all comparative biology, insights of lasting value depend critically on the generation of more complete and more robust phylogenetic trees.

Our emphasis has been largely on the use of plant phylogenies and traits and, to a much lesser extent, on paleontology, population biology, and ecology, and we have yet to mention genomics, developmental biology, or molecular evolution (e.g., Preston & Sandve 2013). Much will be gained by bringing these disciplines to bear on niche evolution. One key issue is the way

in which variation within species (e.g., along environmental gradients) influences the likelihood of biome shifts (e.g., Schluter 1996, Pratt & Mooney 2013). We also see great potential in studies of phenotypic plasticity and population dynamics along the margins of contrasting and rapidly moving environments (e.g., Nicotra et al. 2010, Reed et al. 2011). Most generally, we see these questions as providing an especially promising intersection between ecology and evolutionary biology.

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

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