Title

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Authors

Cavender-Bares, Jeannine
Ackerly, David D
Hobbie, Sarah E
et al.

Publication Date

2016

DOI
10.1146/annurev-ecolsys-121415-032229

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Annual Review of Ecology, Evolution, and Systematics

Volume 47, 2016

Cavender-Bares, pp 433-462

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Annual Review of Ecology, Evolution, and Systematicshttps://doi.org/10.1146/annurev-ecolsys-121415-032229

Jeannine Cavender-Bares,[1] David D. Ackerly,[2] Sarah E. Hobbie,[1] and Philip A. Townsend[3]

[1]Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, Minnesota 55108; email: cavender@umn.edu, shobbie@umn.edu
[2]Department of Integrative Biology and Jepson Herbarium, University of California, Berkeley, California 94720; email: dackerly@berkeley.edu
[3]Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706; email: ptownsend@wisc.edu

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Abstract

Biogeographic origins of plant lineages are often reflected in species functional traits, with consequences for community assembly, diversity, and ecosystem function. The climatic and environmental conditions in which species evolved have lasting influence (legacy effects) through phylogenetic conservatism of traits that underlie community assembly and drive ecosystem processes. Legacy effects that influence community assembly may have direct consequences for ecosystem function or may be linked, owing to lineage history, to traits that impact ecosystems. Evolutionary priority effects, driven by the order of colonization and lineage diversification, as well as migration barriers and historical environmental changes, have shaped the diversity and composition of regional floras and their ecosystem functions. We examine the likely consequences of biogeographic history for plant responses to global change and consider how understanding linkages between biogeographic origins, functional traits, and ecosystem consequences can aid the management and restoration of ecosystems globally in the face of rapid environmental change.

Keywords

biogeographic history, legacy effects, evolutionary priority effects, spectrally derived traits, remote sensing of biodiversity and ecosystem traits, restoration, managed relocation, community assembly

This review addresses how biogeographic history and paleoenvironments have shaped plant form and function and continue to influence the ecosystem processes that provide our life support systems. We focus on how evolutionary innovations and historical contingencies have contributed to modern plant communities, whose qualities can be observed both on the ground and remotely from airborne platforms or satellites. We posit that understanding the context in which plants evolved provides insight into how they will respond to future environmental changes, informing strategies for maintaining a habitable planet.

LEGACIES OF BIOGEOGRAPHIC HISTORY ON COMMUNITIES AND ECOSYSTEMS

Evolutionary and biogeographic history, including past environmental conditions, climate instability, and disturbance regimes, has shaped plant functional traits and influenced the expansion, contraction, migration, and extinction of populations (Braun 1967). These historical factors that underlie the form, function, and distribution of the modern flora have left their imprint in the present, which we collectively refer to as legacy effects. In this review, we consider these effects under two broad headings. First, legacy effects on lineage composition, diversity, and abundance arise because (*a*) dispersal barriers and migration lags have restricted or excluded certain lineages (and their attendant functions) from regional floras (Ordonez & Svenning 2015) and (*b*) evolutionary priority effects, due to arrival and diversification of particular lineages in a region, have created or eliminated opportunities for colonization, expansion, and diversification of later arrivals. Second, legacy effects on functional traits arise when (*a*) adaptations that have evolved in one biogeographic context persist in another or (*b*) distinctive trait syndromes arise early in the history of a lineage and are propagated through diversification and expansion, thereby generating historically contingent impacts on modern ecosystems. These latter two phenomena are captured under the concept of phylogenetic niche or trait conservatism. Legacies resulting from trait conservatism continue to influence community assembly even though the original biogeographic context has changed. Contingent effects of trait syndromes are particularly important when response and effect traits (sensu Lavorel & Garnier 2002) are coupled in locally dominant plant groups, such that disturbance or global change has lineage-specific consequences for ecosystem function in one region that may not occur in other climatically similar systems.

The impact of regional biogeographic processes and historical contingencies on community assembly and diversity has received considerable attention, particularly in relation to the size and composition of the regional species pool (Ricklefs et al. 1999). We extend this perspective to examine the consequences of evolutionary and biogeographic history for ecosystem function. In this review, we focus on the effects of biogeographic origins of lineages, as opposed to phylogeny per se (following Lechowicz 1984). These effects may be strongly concordant in many cases, but they are conceptually distinct and can be decoupled by biogeographic shifts within a clade (such that close relatives evolve under distinct environmental conditions) and biogeographic convergence of distant relatives. As our understanding of species effects on ecosystem processes has improved (Hobbie 2015), it is important to examine the influence of historical processes on lineage and trait composition and diversity.

A key hypothesis that emerges from this analysis is that ecosystem function reflects, in part, legacy effects of the past and cannot be fully predicted from contemporary climatic and geologic settings. Evoking Stephen Jay Gould's (1989) metaphor, if we were to replay the tape of life, might current ecosystems look very different as a consequence of historical contingencies in the evolution and biogeography of plant function? And if so, how might a deeper understanding of this history help us understand today's ecosystems and manage them more wisely in the face of modern environmental change?

To set the stage for this discussion, we summarize changes in the Earth's biogeographic and environmental history that have contributed to the expansion and contraction of modern biomes (**Supplemental Figure 1**). We then discuss legacy effects on lineage composition and trait evolution, highlighting examples of historical processes that influence present-day ecosystem function. Next, we provide a broad overview of innovations in plant function in the context of biogeographic history and examine their ecosystem consequences. We consider how regional processes and trait innovations impact community assembly. Finally, we consider how evolutionary history can be brought to bear on contemporary problems in ecosystem management and restoration ecology in the face of rapid global change. In this brief review, we have sought a balance between case studies that illustrate the important ideas as well as a broad overview of some of the most important aspects of plant function that shape ecosystem processes.

Biological Factors and Processes Shaping the Evolution of Regional Floras

Regional floras have emerged from the diversification and extinction of lineages through time, and the movement of lineages between biogeographic regions, in the context of the Earth's geologic and climatic history. The historical order of lineage diversification and expansion, the idiosyncracies of dispersal and migration processes, and climatic history have contributed to legacy effects on regional composition and diversity. The persistence of ancestral traits and contingencies in trait evolution in plants has also contributed to the assembly, composition, and ecosystem function of modern flora.

Contraction and expansion of major climate zones.

Many lines of evidence point to the combined importance of biome age and available area as drivers of lineage diversification (Fine 2015). Empirical evidence also points to strong evolutionary conservatism of major habitat and biome affiliations; evolutionary transitions between biomes are infrequent relative to diversification and spread within biomes (Crisp et al. 2009). As a result, the expansion and contraction of major climate zones set the stage for the expansion and contraction of lineages. As context for the evolution of contemporary functions of the Earth's biota, we journey briefly through the

Earth's climatic, atmospheric, and tectonic history and sketch out the timing of the expansion of the major biomes (**Supplemental Figure 1**).
Throughout periods of millions to hundreds of millions of years, changes in orbital and solar forcings, along with tectonic processes and resulting volcanic activity, greenhouse gases, and aerosols, have shaped global land and ice area, topography, atmospheric and oceanic circulation, and thus climate. During the Cretaceous (145–65 Ma), most of the terrestrial surface of the Earth was connected and generally warm (Graham 2011). Earth was essentially ice free, and tropical climates extended to high latitudes. Africa, South America, and Australia started separating ca. 120 Ma with complete separation by 100–90 Ma, driving distribution patterns of major plant lineages and altering migration patterns in the Southern Hemisphere. A major asteroid impact 65 Ma, which defines the Cretaceous/Paleogene boundary, led to selective extinctions that influenced the composition and diversity of the Earth's fauna, with lesser impacts on the flora.

Mean annual temperatures in the Late Cretaceous/late Paleocene were 12–14°C warmer at high latitudes than in modern times, and atmospheric CO_2 concentration ([CO_2]) was considerably higher (**Supplemental Figure 1**). The Cenozoic was marked by declining atmospheric [CO_2] and long-term cooling leading up to the more recent large-scale fluctuations in CO_2 associated with Pleistocene glaciations (**Supplemental Figure 1**). Decreases in atmospheric CO_2 along with drainage of many inland seas led to cooling and greater seasonality, favoring deciduousness in angiosperms and gymnosperms and expansion of polar broad-leaved deciduous forest toward more southern latitudes. Massive emissions of methane and CO_2 around 55 Ma from vents in the Norwegian Sea are hypothesized to have caused a global warming event of 5–8°C, known as the Paleocene–Eocene thermal maximum (PETM). The PETM is associated with broad floral shifts, including decreases in conifers and increases in angiosperms, particularly the tropical Fabaceae (the legume clade). Climate warming at this time also temporarily opened northern land bridges that were previously too cold to traverse, promoting transcontinental movement of taxa (McInerney & Wing 2011). About 50 Ma, atmospheric [CO_2] began to decline markedly, likely because tectonic activity increased equatorial land area, where warm temperatures accelerated rock weathering, and CO_2 was captured in bicarbonates that ended up in the ocean and marine sediments (Kent & Muttoni 2013) (**Supplemental Figure 1**). These weathering and sedimentation processes resulted in a net transfer of CO_2 from the atmosphere to the oceans, and particularly in the last 5–7 million years, CO_2 became a strongly limiting resource to plants (Gerhart & Ward 2010, Ward et al. 2005). The large-scale fluctuations in atmospheric [CO_2], temperature, and seasonality during this period played critical roles in terrestrial plant evolution and ecosystem dynamics.

Much of the history of biome expansion is captured in the fossil record (Graham 2011) and further corroborated by fossil-calibrated phylogenies (Donoghue & Edwards 2014). Fossil pollen indicates that angiosperms originated prior to 140 Ma, and molecular evidence suggests the angiosperm origins may go back as far as the Late Triassic, more than 200 Ma (Smith et al. 2010). From these early origins, angiosperms diversified and dominated most of the Earth's terrestrial ecosystems by the Cenomanian ca. 100–90 Ma (Crepet et al. 2004). Plant communities at this time, such as broad-leaved evergreen forests, differed from their modern counterparts, and many contemporary biomes, including grasslands, deserts, and Mediterranean-type ecosystems, did not yet exist. Polar broad-leaved deciduous forests, paratropical rain forests that experienced chilling and/or wet–dry seasonality, tropical forests, freshwater aquatic habitats, herbaceous freshwater wetlands, mangroves, and dune communities were all present (Graham 2011). The lowland tropical rainforests emerged before 64 Ma and were well developed by 58–55 Ma (**Supplemental Figure 1**).

Many of the tree lineages that now define the temperate biome evolved 90–70 Ma (Late Cretaceous) and may have been adapted to short photoperiods and marginal seasonally dry environments (Axelrod et al. 1991). The temperate forest biome became established at high latitudes as the Earth began cooling in the early Paleocene 65–55 Ma (Graham 2011). Climate changes from the middle Eocene onward (Zachos et al. 2001) led to several periods of minor extinctions, including 37 Ma when many terrestrial and marine tropical lineages died out (Prothero 2009). Deciduous or frequently deciduous tree lineages—for example, *Quercus* (oaks), *Ulmus* (elms), *Fagus* (beeches), *Fraxinus* (Ash), *Carya*(hickories), *Prunus* (cherry)—diversified during this cooling period and through the commencement of the ice ages (Hawkins et al. 2014, Manos & Meireles 2015). In particular, *Quercus* radiated and increased markedly in abundance in North America, starting ca. 35 Ma as the temperate forest biome was expanding in middle latitudes (Crepet 1989).

On the basis of the diversification of *Bursera*, a genus of dry tropical flowering shrubs and trees in Mesoamerica, Becerra (2005) concluded that the tropical dry forest biome most likely expanded 30–20 Ma. Shrubland/chaparral, woodland, savanna, and grassland ecosystems increased through the Early–Middle Miocene 24–11 Ma (Graham 1999). Modern Mediterranean climates emerged at similar times on five continents during this period (10–5 Ma) based on paleo evidence (Ackerly 2009, Linder & Hardy 2004) and expanded as recently as 3–2 Ma based on the diversification of *Ruta* (the type genus of the citrus family *Rutaceae*) in the Mediterranean region (Salvo et al. 2010). Lineages previously adapted to low nutrient and/or semiarid conditions diversified to create the modern Mediterranean-type floras (Ackerly 2009).

Grasses formed a minor part of the vegetation in the Eocene 40 Ma, and the earliest grass-dominated habitats developed sometime after 18.5 Ma (Stromberg et al. 2013). Shrublands, chaparral, savanna, and grasslands increased through the Early–Middle Miocene 24–11 Ma (Graham 1999), with C_4 grasses and Crassulacean acid metabolism (CAM) plant lineages expanding largely within the last 8–5 Ma (Edwards & Ogburn 2012, Edwards et al. 2010). Deserts expanded in the Middle Miocene and into the Pliocene around 10–5 Ma (Graham 2011), corroborated by diversification of the Cactaceae 10–5 Ma following the Eocene–Oligocene decline in atmospheric [CO_2] (Arakaki et al. 2011, Hernández-Hernández et al. 2014). Diversification of the most species-rich genera within succulent plant lineages coincided with the expansion of aridity during this period (Arakaki et al. 2011); examples include the African arid environment floras, such as the succulent karoo (Verboom et al. 2014). With late Tertiary global climate cooling, the tundra biome developed and expanded by 7–5 Ma. A brief period of warming in the Miocene (**Supplemental Figure 1**) led to a drying out of the continental interiors, followed by cooling of the global environment; the resulting increase in arid lands may have contributed to the widespread replacement of forests by grasslands and savannas during this time (Prothero 2009). Alpine tundra (páramo) emerged when Miocene cooling was augmented by the high elevations attained, for example, in the Andes after 10 Ma (Graham 2011).

Legacy effects on regional species composition and diversity.

As climate zones expanded at different times in the Earth's history, particular lineages proliferated in the flora of the respective biomes. Examples from the Americas include *Quercus* in temperate forests, *Bursera* in tropical dry forest, and Cactaceae in deserts. The diversification of such clades largely within biomes reflects the importance of niche conservatism. Evolutionary conservatism, coupled with key innovations, sets the context for our discussion of legacy effects on the composition and diversity of regional floras, as well as our subsequent discussion of legacy effects from trait and niche conservatism.

Evolutionary priority effects.

Environmental change creates new ecological and evolutionary opportunities. Lineage(s) that can persist under novel conditions have an opportunity to diversify rapidly and occupy a region or biome, potentially limiting ecological and evolutionary opportunities for lineages that arrive later. We refer to this phenomenon as the evolutionary priority effect, analogous to the ecological priority effect arising from the order of arrival of species within a community. Successful lineages presumably possess traits that allowed them to persist, radiate, and dominate. These traits may have had important ecosystem consequences, or the lineages may have brought along other important functional traits with ecosystem outcomes.

One potential example of the legacy of evolutionary priority effects can be seen in the dominance of oaks (*Quercus*, Fagaceae) in North American forests. As the Earth cooled dramatically some 35 Ma, following a longer-term cooling and drying trend (Zachos et al. 2001), tropical taxa in North America went locally extinct, contracting to lower latitudes (Crepet & Nixon 1989, Graham 2011) and creating opportunities for expansion, speciation, and adaptive radiation of other lineages in the newly created temperate zone. The oaks, in particular, exploited this opportunity. Two oak clades diversified rapidly (the red and white oaks) under the cooler and drier climates, possibly because they had previously evolved deciduousness and leaf abscission responses to stress in seasonal environments. Interestingly, both of these groups radiated and expanded their ranges with nearly equal diversity and extent. Their parallel adaptive radiation into many different habitats left a legacy of oak-dominated temperate forests in North America (Cavender-Bares 2016, Hipp et al. 2014).

Oaks contribute more biomass and diversity to naturally assembled forests of North America (United States and Mexico) than any other lineage (Cavender-Bares 2016). They bring a suite of traits with ecosystem consequences beyond biomass, including deep roots, fire tolerance, large seeds that are important food sources for wildlife (and historically for Native Americans), ectomycorrhizal associations, dense wood, and foliar defense traits (condensed tannins/phenolics) that influence herbivory and decomposition. We hypothesize that this radiation exemplifies an evolutionary priority effect, in which early arrival and diversification may have preempted the expansion of other lineages. Although some of the traits listed above may have contributed to the migration, expansion, and diversification of oaks, others may have "come along for the ride" because they were present early in the diversification of the group and subsequently persisted. The expansion and dominance of this group have left an important legacy on north temperate forest ecosystems, reflecting lineage history and not necessarily directly predictable from environmental factors.

Plant colonization of Hawai'i by natural dispersal, followed by more recent human introductions, exemplifies legacy effects in the assembly of an isolated flora. Colonization by the native flora was followed by evolutionary and geographic diversification and is hypothesized to have limited the niche breadth of more recently introduced species. Native species tend to be climate generalists, and early colonizers, facing little competition, expanded and adapted to a broad spectrum of environments. For example, on Mount Haleakala on the island of Maui, native species inhabit a broad range of habitats, from warm, moist lowlands to cool, arid higher elevations (**Kitayama & Mueller-Dombois 1995**). In contrast, introduced species are limited to those habitats that have been disturbed, either by natural canopy dieback of native forest at lower elevations or by grazing at higher elevations, and are largely absent from undisturbed montane forests at middle elevations. Furthermore, the introduced species exhibit greater climate specialization and more restricted ranges than the native species, with tropical-derived lineages in the lowlands and those with temperate affinities at higher elevations (**Kitayama & Mueller-Dombois 1995**). Thus, the introduced species are constrained by their prior adaptations and biogeographic affinities and have less opportunity to expand their niches, perhaps because the island communities are more ecologically saturated (**Kitayama & Mueller-Dombois 1995**). The order of arrival created a legacy that may have limited niche expansion in latecomers, analogous to a process that may have been important historically in the assembly of regional biomes.

***Dispersal barriers*.**

Dispersal processes and biogeographic barriers influence which taxa are present in regional floras and thus shape the spectrum of functional traits that contribute to local and regional ecosystem processes. Over millions of years, most taxa likely can disperse on a continental or subcontinental scale, so the entire continent provides the relevant regional pool for community assembly. At shorter timescales, only species that occur within tens or hundreds of kilometers may be relevant. At any scale, dispersal processes and barriers that shape the regional species pool may have direct consequences for the structure and function of local ecosystems. Many Northern Hemisphere lineages have never dispersed to the Southern Hemisphere (e.g., **Axelrod et al. 1991**), possibly leading to distinct ecosystem function of communities under analogous temperate climates. The recent rapid spread of exotic pines introduced by humans in New Zealand and South Africa, and other invasive species with novel functional types, attests to potential impacts of these dispersal constraints (**Mack 2003**).

Large-scale invasions such as pines in the Southern Hemisphere challenge the ideas that contemporary communities are saturated and that priority effects limit the establishment of new taxa. In some cases, invasions may be promoted by anthropogenic disturbance; thus, environmental changes may also be involved. The hypothesis of release from enemies as a major factor contributing to invasions exemplifies the importance of dispersal limitation and the unique events that transpire following long-distance arrival of taxa from other continents.
Within continents, migration between isolated but similar habitats may be prevented by lack of suitable habitat in between. For example, seasonally dry tropical forests (SDTFs) in South America have distinct floristic composition in separate locations, perhaps because species adapted to a lengthy dry season cannot migrate through wet forest owing to inferior competitive ability in wetter forests or lack of defense mechanisms against wet forest pathogens (**Pennington et al. 2009**). Different taxonomic composition in separate SDTF locations will likely result in contrasting ecosystem properties, particularly if functional traits differ among these groups of taxa.

Island floras, and island-like floras on edaphically specialized substrates, are particularly influenced by dispersal limitation and thus consist of only a subset of potentially contributing mainland lineages. Long-distance dispersal traits common in island floras, such as small seeds with dormancy, may be prerequisites for colonization. For example, in the Hawai'ian islands, native plant species that arrived naturally via dispersal are consistently small seeded (R. Montgomery & R. Ostertag, personal communication). Dispersal traits may be associated with other traits that influence, for example, other trophic levels and the set of herbivores that can be supported. Consequently, plant functions represented by large seeded species on the mainland may be missing from islands. In contrast, plant species introduced by the Polynesian people tend toward large seeds and are functionally distinct (**Ostertag et al. 2015**), demonstrating that alternative functions can be maintained under the same environmental constraints.

The native flora of Hawai'i also lacks flammable grasses, also likely a consequence of dispersal. Consequently, native Hawai'ian grassland ecosystems experience lower frequency of fires and fires with smaller extents than grasslands in other regions of the globe, with major consequences for nutrient cycling and carbon dynamics (**Mack et al. 2001**). They are also highly susceptible to invasion by flammable African grasses, introduced by humans, which have altered fire regimes and promoted their own success via positive feedbacks on successional dynamics (**D'Antonio & Vitousek 1992**).

***Connectivity of land masses*.**
The distributions of taxa across continents are also influenced by the timing of lineage evolution with respect to plate tectonic history, due, in part, to dispersal opportunities. The tropics are home to old angiosperm clades, many of which arose before the continents separated, so the clades are shared across all three tropical regions: the Americas, Africa, and Australasia [subsequent long-distance dispersal also contributes to this pattern (**Dick et al. 2007**)]. Vicariance of the Gondwanan biota has served as textbook evidence for the importance of ancient connectivity, although there, too, recent

evidence points to an important role for long-distance dispersal across the southern oceans (Verboom et al. 2014). The north temperate flora also has major lineages shared across continents, although in this case episodic land bridges and high-latitude connectivity have played important roles in facilitating periodic dispersal (Tiffney & Manchester 2001). In contrast, Mediterranean ecosystems, subtropical dry forests, and deserts arose more recently when continents were further apart, and these independent origins are presumably a major reason for their floristic dissimilarity across continents.

***Past environment, climate instability, and migration lags*.**

Climate instability compounds the effect of dispersal limitation. Differences in geologic histories, locations of mountain ranges, and climatic histories have led to different extinction rates and dispersal barriers in Europe and Asia, influencing diversity, composition, and ecosystem functions (Ordonez & Svenning 2015). Glaciation cycles and time lags in vegetation shifts following glacial retreat have been implicated in deficits of plant diversity, including underrepresentation of species with limited long-distance dispersal ability, seed plants compared with ferns, and small-range species. Recolonization from glacial refugia has influenced which species and functions are represented because slow migration rates impeded many taxa from occupying the climatic regions to which they were well suited (Normand et al. 2011). Migration lags explain reductions in observed, relative to potential, plant functional diversity (for seed weight, plant height, specific leaf area, and stem tissue density) in areas with high climatic instability far from major temperate glacial refugia (Ordonez & Svenning 2015). Glacial cycles have also been linked to species range sizes at large scales, likely because when extinction is high, more habitat becomes available for those few persistent species or the recolonizing species that do arrive (Morueta-Holme et al. 2013). Consequently, species and functions may drop out due to major climatic disturbances and dispersal barriers.

Legacy effects from trait and niche conservatism.

The persistence of ancestral traits, and the resulting niche conservatism, has important consequences for the assembly of regional floras and for the contribution of individual taxa to ecosystem properties. Niche conservatism is the tendency for organisms to maintain the traits and environmental tolerances (i.e., the niche) of their ancestors. Organisms tend to establish and persist in environments to which they are already well adapted, leading to stabilizing selection and trait conservatism (Ackerly 2003). During periods of climate change, if species are able to track suitable conditions, existing traits may be maintained. Conversely, expansion of novel climates in which lineages adapted to the new conditions are absent sets the stage for evolutionary innovation.

For example, as temperate climates developed during the Cenozoic, tropical lineages lacking freezing tolerance could not invade and diversify in the temperate zone. Relatively few lineages evolved the necessary traits to make this transition (Zanne et al. 2014), contributing to the latitudinal diversity gradient (Fine 2015, Latham & Ricklefs 1993, Wiens & Donoghue 2004). Crisp et al. (2009) found that 96% of speciation events in Southern Hemisphere lineages showed biome or habitat conservatism, even when coupled with long-distance dispersal events. Niche conservatism likely explains the strong geographic structuring of *Bursera* in SDTFs of Mesoamerica and the absence of this clade in non-SDTF habitats (De-Nova et al. 2012).

Even when taxa adapt to new environments, conservatism of functional traits and legacies of past environments have consequences for ecosystem function. Across Mediterranean-type ecosystems that differ in soil nutrient availability, plants retain lineage-specific foliar chemical composition and stoichiometry (**Stock & Verboom 2012**). Fabales, Rosales, and Caryophyllales have relatively high foliar nitrogen, and Asterales and Caryophyllales have relatively high foliar phosphorus, whereas Ericales, Fagales, and Myrtales have low foliar nitrogen and phosphorus. Thus, foliar nutrients, which influence decomposition and nutrient cycling rates, depend in part on which lineages were available to colonize these systems and the conservatism of their functional traits.

***Contingent trait syndromes*.**

When two or more traits evolve early in the history of a lineage, they may create associations that neither are due to an intrinsic functional linkage between the traits (i.e., as part of a syndrome or strategy) nor represent responses to the same selective factors. The associations between such traits may be somewhat idiosyncratic and contingent on this early history, and may then be propagated through subsequent diversification. The resulting suite of traits in the descendent taxa cannot be directly attributed or explained as a response to the environment in which species currently occur or by biochemical, structural, or adaptive constraints. Unpredictable ecosystem consequences may emerge in cases in which traits are coupled as a result of shared evolutionary history, particularly when one is a response trait and another is an effect trait.

One example occurs within the American live oaks (*Quercus* subgenus *Virentes*), a lowland evergreen oak lineage that, like other oaks, has ectomycorrhizal associations and deep roots that allow access to deep water reserves during prolonged drought. They also produce a belowground swollen stem tuber to which lipids and nutrients from the cotyledons are transferred in the first year of growth. These tubers protect the plant against aboveground herbivory and desiccation. Through long-distance dispersal, one of these species (tropical live oak, *Quercus oleoides*) arrived in the seasonal dry forest region of Guanacaste, Costa Rica, during the Middle Pleistocene (**Cavender-Bares et al. 2015**). They are able to survive the prolonged dry season, likely due to groundwater access, protective tubers, and leaves with high hydraulic resistance (**Cavender-Bares et al. 2007**). However, most other seasonally dry tropical trees that occur in the same region tend to have deciduous leaves, dormant seeds, and arbuscular mycorrhizae (AM). The evergreen canopy, ectomycorrhizal associations, desiccation intolerant seeds, and masting behavior contributed by *Q. oleoides* in this community have important ecosystem consequences in terms of nutrient cycling, productivity, and diversity of other trophic levels (**Kissing & Powers 2010**, **Klemens et al. 2011**).

The *Eucalyptus* clade in forests throughout Australia is another relevant lineage in this context. *Eucalyptus* trees are adapted to the low-nutrient soils of the region as well as to drought and fire, in part due to their lignotubers that store starches and other food reserves belowground and their sclerophyllous, long-lived leaves. In addition to their physiological ability to tolerate low nutrients and hot, dry summers, they have flowers that produce copious nectar for their bird and bat pollinators, as well as flaky bark and insect-repelling oils that promote fire (Williams & Woinarski 1997). This particular constellation of traits is singular to the lineage, and no obvious developmental, architectural, or adaptive constraints connect all of them. As a consequence of their bark structure, *Eucalyptus* tend to lack epiphytes, which may limit total litter production (Muzika et al. 1987) and possibly water and nutrient capture (Van Stan et al. 2015); the pollination syndrome impacts the food web structure and biodiversity of other trophic levels; and their fire-promoting behavior makes eucalypt forests functionally quite distinct from, for example, wind-pollinated oak forests in similar climates of the Iberian peninsula or California (Madeira et al. 1989).

Major Innovations in Trait Evolution and Their Implications for Ecosystem Function

The biogeographic origins and histories of plant species have shaped their functional traits in ways that persist despite subsequent evolution in different environmental contexts. A central thesis of this review is that ecologically important plant traits have passed through critical periods of evolutionary innovation and expansion, and that traits shaped by paleoenvironmental contexts continue to impact ecosystems today (**Supplemental Figure 2**). In this section, we examine major periods in plant evolutionary history and focus on functional trait innovations for resource acquisition and environmental tolerance that have well-understood consequences for ecosystem function.

Current plant function is influenced by innovations through many periods of plant evolution: ancient mechanisms for acquisition of nutrients and water that accompanied the transition to land; ancestral traits, especially of woody lineages (Cretaceous and earlier), that have become widespread across modern ecosystems; important innovations accompanying cooling and atmospheric change in the Paleogene, which shape modern biomes; and more recent adaptations, especially to aridification during the Neogene, or even more recent postglaciation shifts during the Pleistocene (e.g., photoperiod cues; see the section on Phenological Responses to Seasonality). Physiological tolerances and attributes that arose in one historical biogeographic context might influence assembly processes in new contexts and influence diversity, composition, and ecosystem function (**Supplemental Figure 2**).

Traits involved in the responses of organisms to their environments (response traits) are frequently distinguished from those that have consequences for ecosystem functions (effect traits) (Lavorel & Garnier 2002) (although many traits have functions associated with both environmental responses and effects on ecosystems; see **Supplemental Table 1**). For example, species with dormant seeds, which allow them to avoid drought and freezing, are frequently selected for in highly seasonal environments; however, the ecosystem consequences of the presence of these species derive more from plant size, nutrient stoichiometry, and fuel-loading potential than from seed physiology. If response and effect traits are generally correlated, as a consequence of either biophysical constraints or natural selection, as is seen within suites of traits that compose the leaf economic spectrum (Wright et al. 2004), we can predict ecosystem consequences of environmental filters influencing community assembly. However, traits associated with major clades can be correlated in some systems but not in other systems owing to historical contingency, particularly if traits have only one or a few shared origins. This scenario links evolutionary priority effects to historically contingent effects on ecosystems that might differ across regions.

Water transport.

Wood (secondary xylem) evolved to move water efficiently against the pull of gravity, allowing a multilayered canopy and more efficient light capture. Homoxylous wood (tracheids only) evolved in gymnosperms during the Devonian and expanded with their radiation in the Carboniferous 300–400 Ma (Gerrienne et al. 2011). Heteroxylous wood (with fibers, vessels, and parenchyma) in angiosperms appeared during the Albian (Philippe et al. 2008), ca. 110 Ma. The greater transport efficiency of angiosperm vessels enhanced gas exchange and productivity but may also have increased the susceptibility to drought (Choat et al. 2012). Gymnosperms use narrow and short tracheids for water transport and have specialized pit membrane structures that maintain conductivity while preventing conduit blockage due to air seeding, a danger that increases with drought (Pittermann et al. 2005). Angiosperm vessels are large with high conductance, and they rely on highly resistant intervessel pit membranes to prevent the spread of emboli (air bubbles) in the xylem. Innovations in the hydraulic architecture of wood are associated with novel leaf morphologies and functions. Decreasing CO_2 during the Late Devonian ca. 400 Ma is implicated in the evolution of megaphyllous leaves in gymnosperms (Gerhart & Ward 2010, Graham 2011) with higher stomatal densities, transpiration rates, and capacity for cooling, characteristics that are associated with increased photosynthetic capacity (Sack & Holbrook 2006). Angiosperms also underwent major evolutionary shifts in leaf size and hydraulic architecture associated with their rise to dominance. During the Cretaceous, angiosperms were small shrubs and herbs in the understory of coniferous forests and represented only a minor element of the flora (Bond & Scott 2010). Later, angiosperms evolved new leaf and stem hydraulic structures, including increased venation, stomatal densities, and larger conduits (Brodribb & Feild 2010). Vein (Brodribb & Feild 2010) and stomatal (Franks & Beerling 2009) densities increased dramatically in angiosperms from the Middle to Late Cretaceous (ca. 100 Ma) and diversified as atmospheric [CO_2] declined (**Supplemental Figure 1**). These leaf hydraulic properties would have increased water transport and conductance, permitting higher gas exchange rates (Brodribb & Feild 2010). Other changes in leaf physiology, including increased leaf nitrogen, occurred in parallel. Higher transpiration rates associated with changes in leaf hydraulic properties may have been critical in recycling water and bolstering precipitation in tropical rainforests, thereby supporting higher productivity (Boyce et al. 2009).

Variation in water availability with changing climate and the emergence of new biomes drove further shifts in hydraulic architecture. Vulnerability to cavitation has diverged widely as a function of water limitation across species (Maherali et al. 2004); dry periods drove the adaptation of cavitation-resistant xylem in the Cupressaceae during the past 30 Ma (Pittermann et al. 2012). The expansion of arid and Mediterranean environments 3–7 Ma would have favored more drought-resistant vascular anatomy. Within angiosperms, vasicentric tracheids, documented in at least 66 families globally, have been hypothesized to maintain hydraulic function during periods of low water availability (Carlquist 1985), although timing of this innovation is not established.

Vascular transport plays a major role in the global hydrologic cycle that drives upward of 80% of evapotranspiration over land, influencing atmospheric circulation and precipitation patterns (Jasechko et al. 2013). Relationships between xylem architecture, specific leaf area, leaf area index, and leaf habit influence evapotranspiration: Higher leaf area index and extended leaf duration in evergreen gymnosperms lead to greater interception of precipitation and may offset lower hydraulic conductivity to minimize differences in stand-level evapotranspiration between deciduous angiosperms and evergreen gymnosperms (Augusto et al. 2015).

Carbon uptake and photosynthetic pathways.

C_3 photosynthesis evolved with the earliest cyanobacteria and was harnessed by the green plant lineage as plants colonized land in an atmosphere with likely much higher [CO_2] than present. At low atmospheric [CO_2] and with increasing temperatures, RuBisCO, the carboxylating enzyme, frequently binds O_2 instead of CO_2 in a wasteful process termed photorespiration, whereby newly fixed carbon is oxidized without producing ATP or sugar. C_3 photosynthesis is an efficient process if [CO_2] in plant tissue is high, but plants can become carbon limited under low atmospheric [CO_2].
Earth probably reached CO_2 concentrations of approximately 180–190 ppm during glacial maxima in the Pleistocene, and these were among the lowest values that existed on the planet throughout the evolution of land plants (Gerhart & Ward 2010). Stable carbon isotopes from ancient trees in the La Brea tar pit at the end of the last glacial maximum, when [CO_2] was lower than today (180–200 ppm), indicate that conifers (*Juniperus*) were operating close to the CO_2 compensation point for life cycle completion, suggesting carbon starvation. Carbon starvation was a legacy effect of evolution in a time when the Earth's atmospheric [CO_2] was much higher (**Supplemental Figure 1**) and likely represented a significant fitness cost to plants as [CO_2] declined (Gerhart & Ward 2010).

The C_4 photosynthetic pathway is hypothesized to have first emerged when [CO_2] was declining in the Earth's atmosphere 30–20 Ma and pathways that reduced photorespiratory losses were favored (Keeley & Rundel 2003, Sage et al. 2011). It evolved independently in at least 8 disparate angiosperm clades, including in the grasses, sedges, Caryophyllales, *Cleome*, *Hydrilla*, Zygophyllaceae, and Heliantheae, with ca. 70 origins throughout these clusters (Edwards & Ogburn 2012). As [CO_2] continued to decline to values lower than today's levels (7–4 Ma), novel origins and diversification of those lineages rapidly increased, causing the ecological prevalence of C_4 plants to grow explosively (Edwards & Ogburn 2012). The ecological expansion of C_4 plants at this time is readily detected in ^{13}C signatures of plant and herbivore fossils (Ehleringer et al. 1997, Gerhart & Ward 2010, Sage et al. 2011).

C_4 photosynthesis prevents or minimizes direct exposure of RuBisCO to O_2 by anatomically isolating RuBisCO from O_2. C_4 species generally do not respond to elevated CO_2 because of their low rates of photorespiration. Higher temperatures and lower [CO_2] thus tend to favor C_4 species. The C_4 pathway also allows plants to close or partially close their stomates, reducing water loss and increasing water use efficiency (WUE). They also have higher photosynthetic nitrogen use efficiency (PNUE) because the RuBisCO enzyme in C_4 plants fixes CO_2 with less binding affinity and thus with greater efficiency than in C_3 plants, thereby allowing C_4 plants to assimilate the same amount of carbon with less nitrogen investment in RuBisCO. Differences between C_3 and C_4 plants in PNUE, WUE, and responsiveness to increased [CO_2] and temperature have consequences for ecosystem-level transpiration, net primary productivity (NPP), and nutrient cycling. For example, C_4 species are superior competitors in low-nitrogen grasslands and, in turn, produce low rates of nitrogen mineralization because of the chemistry of their litter (**Wedin & Pastor 1993**). In addition to nitrogen availability, the distribution and relative NPP of C_4 and C_3 grasses are closely associated with precipitation patterns, with higher C_4 abundance in drier sites (e.g., **Epstein et al. 1997**, **Pau et al. 2013**). These community and ecosystem consequences represent legacy effects of a functional trait that was shaped by historically low [CO_2].

CAM photosynthesis also concentrates CO_2 around the RuBisCO enzyme and is the most efficient pathway for minimizing water loss in hot arid regions. CAM allows plants to fix CO_2 at night and store carbon compounds in photosynthetic cell vacuoles until light is available for activation of RuBisCO. Consequently, CAM plants close their stomates during the day, reducing water loss. CAM first evolved, ca. 200 Ma, in the aquatic lycopod *Isoetes* that occurs in shallow-water habitats. Numerous independent origins of the CAM pathway occurred much later, and in the same time frame as the origin, diversification, and expansion of C_4 lineages (**Edwards & Ogburn 2012**). This pattern is exemplified by the diversification of desert succulents in the Caryophyllidae (Aizoaceae, Cactaceae, and Portulacaceae), Rosidae (Crassulaceae and Euphorbiaceae), and Asteridae (Asclepiadaceae and Asteraceae) (**Arakaki et al. 2011**, **Hernández-Hernández et al. 2014**). Globally, CAM is found in lycopods, ferns, gymnosperms (e.g., *Welwitschia*), and numerous monocot and dicot lineages (**Edwards & Ogburn 2012**, **Keeley & Rundel 2003**).

If the global expansion of arid environments 7–3 Ma led to novel origins and the diversification of the CAM photosynthetic pathway, it may have legacy effects in other environments in which the pathway was also beneficial. For example, CAM is widespread in tropical forest epiphytes, which experience physiological drought associated with their aerial growth habit. Diversification of the bromeliad family (Bromeliaceae), in which the ephiphyte habit occurs with high frequency, appears to have occurred concurrently with or after the expansion of aridity (**Bouchenak-Khelladi et al. 2014**). The appearance of CAM photosynthesis within the lineage may have enabled transitions to the epiphytic habit, making epiphytic behavior ultimately a legacy of global expansion of arid environments 10–5 Ma (**Arakaki et al. 2011**). By persisting in aerial environments in which non-CAM plants cannot survive, CAM epiphytes contribute to ecosystem NPP and to ecosystem water storage. For example, the epiphytic bromeliad *Tillandsia* (Spanish moss) contributes significant annual litter production (Muzika et al. 1987) and captures substantial water and nutrients in southeastern U.S. temperate forests (Van Stan et al. 2015).

Plant responses to disturbance.

Fire and herbivory are perhaps the two primary factors that cause destruction of aboveground vegetation, followed by wind-throw and other physical disturbances. Fire was frequent in the Cretaceous, and numerous angiosperm lineages developed adaptations that enhance regeneration following disturbance, including resprouting and storage tissues (Bond & Scott 2010). The role of fire versus other disturbances in the evolution of these strategies is not well resolved. Climatic changes in the Late Miocene likely increased the incidence of fires (Keeley & Rundel 2003). Efficient hydraulic transport in angiosperms would have promoted rapid regeneration and high productivity (Bond & Scott 2010, Brodribb & Feild 2010); increased fuel loads together with increasing atmospheric [O_2] may then have contributed to novel fire regimes. The canopy openings created by fire would have allowed angiosperms to invade the poorly lit understories of dense coniferous forests that covered the Earth's land masses and may have contributed to the rise of angiosperms.

The regeneration traits (resprouting, belowground storage) that evolved in some lineages early in angiosperm evolution (i.e., during the Cretaceous) promote persistence in fire-dominated present-day ecosystems. It is of interest that the same lineages in which these attributes emerged still maintain them, whereas lineages lacking these traits still appear to lack them. Even as major climatic axes of the niches of these taxa would have changed over the course of the climate change that has occurred since then, the traits that influence the disturbance regime in which they persist appear to have been conserved, at least to some extent. At the local scale, lineages that diverged more than 80 Ma assembled into contrasting treatments in a 40-year fire frequency experiment at Cedar Creek, Minnesota, that demonstrated the deep legacy of fire-adapted traits (Cavender-Bares & Reich 2012). For example, fire-adapted tree species in the Fagaceae, with thick bark and resprouting ability, or herbaceous Asteraceae and Poaceae species that invest heavily in belowground biomass, co-occurred in frequently burned ends of the gradient. In contrast, fire-intolerant woody species in the Rosaceae or vines in the Vitaceae assembled on the unburned end. Plant species thus show phylogenetically conserved patterns in community assembly, likely driven by traits that emerged when the Earth's fire regime was very different than it is today (**Supplemental Figure 1**). These traits in turn influence rates of soil nutrient and carbon cycling in savanna ecosystems (Dijkstra et al. 2006, Norris et al. 2013).

Belowground storage and regrowth mechanisms also facilitate recovery from damage by large herbivores. Mammalian grazers likely contributed to the spread and maintenance of grasslands (Stromberg et al. 2013). Structural attributes, including well-protected buds, spines, lignin and condensed tannins, and silica (phytoliths) in grasses, deter herbivores and also influence litter quality, making it more recalcitrant to microbial decomposition. Innovations in defensive chemistry are thought to have evolved in concert with plant-feeding insects in an evolutionary arms race to deter herbivory (Agrawal 2007, Ehrlich & Raven 1964). Plants have evolved an enormous diversity of defensive chemicals, which may be toxic, repellent, or antinutritive for herbivores of all types and include cyanogenic glycosides, glucosinolates, alkaloids, and terpenoids, as well as macromolecules, including latex or proteinase inhibitors (Mithöfer & Boland 2012). Shorter-lived leaves with higher nitrogen content and faster photosynthesis are also more susceptible to herbivory and thus tend to have more secondary compounds (Coley 1983). Trade-offs between growth rate and defense are thought to be widespread but have only occasionally been documented experimentally (Fine et al. 2006). Leaf lifespan, nutrient concentrations, and defense chemistry are well-known to influence litter quality and decomposition rates (e.g., Cornwell et al. 2008, Hobbie et al. 2006).

Temperature tolerance.

Plants draw on a variety of morphological and biochemical mechanisms to dissipate heat. Plants that emit isoprene (an alkene, i.e., a hydrocarbon with carbon–carbon double bonds) are chemically able to dissipate excess thermal energy that occurs in intense pulses and are thus better able to tolerate rapid heating of leaves (heat flecks) than non-emitters. The capacity for isoprene emission evolved independently many times in both gymnosperms and angiosperms. Although the isoprene synthase gene family probably has a single origin, the angiosperm isoprene synthases are distinct from those in gymnosperms. The capacity to emit isoprene reflects both biogeographic origins and phylogenetic lineages and is most common in trees, particularly oaks and aspens, which are subject to intense sunlight and heat gain that can vary within short periods (e.g., Sharkey et al. 2008). All Fagaceae (especially *Quercus*) and all Salicaceae (especially *Populus* and *Salix*) are emitters, as are many Fabaceae and Myrtaceae (Dani et al. 2014). Isoprene emission does not necessarily help plants to tolerate sustained high temperature stress; thus, species from hot deserts do not emit significant isoprene. In contrast, the wet tropics, where evaporative cooling is reduced due to high humidity, have many isoprene-emitting species. Isoprene emissions are energetically costly, and the distribution of the capacity for isoprene emission among lineages may depend on the balance between costs and benefits (Sharkey et al. 2008). Isoprene emissions influence atmospheric hydrocarbon chemistry and tropospheric ozone production, and plants emit much more hydrocarbon into the atmosphere than human activities, especially during extended warm weather (e.g., Sharkey et al. 2008). Although isoprenes are not greenhouse gases themselves, their influence on hydrocarbon, nitrous oxide, and ozone chemistry indirectly increases the greenhouse effect. Isoprene emission by terrestrial plants, which totals approximately 2% of carbon fixed during photosynthesis, reduces the terrestrial carbon sink by as much as 0.5 Pg C/year (Dani et al. 2014).

Temperature responses of the photosynthetic system also reflect climatic origins. Catalytic efficiencies of RuBisCO in both C_3 and C_4 are higher in species originating in cool environments relative to those originating in warm environments, and CO_2-binding affinities are higher in C_3plants from warm climates, indicating that RuBisCO has evolved to improve plant performance in the climatic environments in which they occur

(Sage 2002). The alignment of photosynthetic efficiencies with climatic origins may be important for competitive ability and ecosystem productivity as climates change.

Adaptations to low temperatures are critical for persistence in cold climates. Freezing temperatures can cause lethal injuries in living plant tissues, if freezing occurs inside living cells, and can limit the long-distance transport of water and sugars by freezing water in the xylem conduits and increasing viscosity of the phloem (Cavender-Bares 2005). With cooling of the Earth's climate and expansion of the temperate zone, plants have evolved three major options for persistence: (*a*) herbaceousness, or for woody plants, (*b*) evergreen habit and cold-temperature resistance, or (*c*) deciduousness and winter dormancy. Long-lived needle-shaped leaves evolved early in gymnosperms, but some gymnosperm lineages (e.g., *Ginkgo*, *Glyptostrobus*, *Metasequoia*, *Taxodium*) evolved deciduousness in response to cooling in the Paleogene. The broad leaves of angiosperms would have been evergreen in the Late Cretaceous when tropical biomes dominated the Earth. Deciduousness in angiosperms may have evolved at higher latitudes in the Northern Hemisphere as an adaptation to short photoperiods, before the cooling/drying period of Eocene and Oligocene (Axelrod et al. 1991). At lower latitudes, deciduousness may have first evolved in response to seasonal drought. As the climate cooled and the temperate zone expanded, deciduousness would have been favored by freezing winter periods. Zanne et al. (2014) hypothesized that evolution of deciduousness in angiosperms frequently followed shifts in climate, suggesting it may have often been an adaptation to freezing rather than an exaptation [a trait that evolved prior to the novel environment but enhanced fitness within it (Gould & Vrba 1982)]. Mechanisms of freezing tolerance in evergreen plants, including supercooling, freezing resistant leaves (or needles), and narrow tracheids or vessels, allow persistence in cold and freezing temperatures. These mechanisms, as well as deciduousness in trees, contribute to the maintenance of living carbon stocks in biogeographic regions with freezing winters. However, longer-lived evergreen leaves have very different anatomical properties, nutrient content, and morphology captured by the leaf economic spectrum and consequently have contrasting influence on decomposition and nutrient cycling (Cornwell et al. 2008) (see section on Nutrient Cycling).

Cold climates may also favor high leaf nitrogen and phosphorus content relative to carbon content to offset reduced efficiency of enzymes and metabolites (Reich & Oleksyn 2004). In particular, cold-adapted species may compensate for reduced enzymatic rates with higher enzyme concentrations. Within species, when populations native to sites differing in temperature are grown under common garden conditions, populations from colder habitats often exhibit greater leaf nitrogen and phosphorus (Chapin & Oechel 1983). This paradigm would lead to the hypothesis that tropical lineages from highly weathered soils would have legacy effects of high phosphorus use efficiency and low nitrogen use efficiency after migration or radiation into the temperate zone, whereas co-occurring taxa originating from the temperate zone would retain high nitrogen use efficiency but comparatively lower phosphorus use efficiency. To our knowledge, this hypothesis has not been tested.

Phenological responses to seasonality.

Lechowicz (1984) first suggested that phenological differences among co-occurring deciduous tree species were linked to the biogeographic origins of their immediate ancestors. Phenological adaptations to seasonality may be associated with biogeographic origins and may also evolve rapidly, either eroding legacy effects or causing legacy effects to be very recent. Fitness costs associated with mistiming are expected to be high because blooming or leafing out too early or too late can lead to extensive tissue damage or death due to frost or drought, resulting in strong selective pressure and rapid evolution. Considerable evidence for genetically based intraspecific variation in phenology associated with climate of origin supports this perspective. However, there is evidence for phylogenetic conservatism in phenology (Davies et al. 2013, Willis et al. 2008). Davies et al. (2013) point out this potential paradox and argue that closely related species might share similar phenologies either because close relatives share the same genetic mechanisms driving phenology and/or because they grow in, and are adapted to, similar environments. It seems reasonable to expect that the nature of cues used for phenological responses to seasonal changes would be linked to origins. A review of genetic and physiological mechanisms involved in phenological responses to seasonal changes found that flowering and leafing cues in over half of species examined, with a strong temperate bias, were linked to photoperiod or irradiance, which vary with latitude; warming and precipitation were other important cues (Pau et al. 2011). At high latitudes, photoperiod and favorable climate for growth are closely linked, making photoperiod a reliable cue for boreal-origin lineages, even though the offset between leaf-out and changes in day length would have shifted repeatedly through glaciation cycles. In contrast, tropical-origin species might be expected to have a greater propensity to cue to temperature or precipitation rather than photoperiod. If these expectations are borne out, it is likely that biogeographic origins of recent ancestors of co-occurring plants in an assemblage explain the phenological differences among them. Recent origins thus provide context for the kinds of changes taxa can be expected to respond to and the likely nature of adaptive changes. Ecosystem consequences of contrasting origins can also be considered. For example, contrasting phenological attributes of co-occurring species arising from distinct origins, such as cool- and warm-season grasses or evergreen and deciduous trees, may contribute to complementarity in resource use, resulting in higher productivity of ecosystems than might be expected if all shared equivalent phenological patterns.

Nutrient acquisition.

The problem of acquiring nutrients from soil is as ancient as land plant colonization. Adaptations to acquire specific nutrients arose in different ways in different times and places, with a small number of major innovations that allowed plants to persist and thrive. Unlike the acquisition of carbon, these innovations are not readily associated with specific periods or places in Earth history; rather, they may reflect heterogeneity in nutrient availability related to factors such as parent material and degree of weathering, in turn related to climate and age of ecosystem development (Lambers et al. 2008). Several important nutrient acquisition traits evolved early in the history of terrestrial plants (**Supplemental Figure 1**). AM likely evolved concurrently with colonization of land by plants ca. 500–450 Ma and persist in 80% of extant plant taxa (Wang & Qiu 2006). Because AM symbioses are so ancient in plants, they are widespread across many lineages globally (a frequent characteristic of the ancestral state in character evolution). Ericoid mycorrhizae (EM) and ectomycorrhizae (ECM) evolved later, in the Cretaceous, and are derived states that characterize fewer lineages. EM evolved in association with plants in the Ericales (the heaths) (140–90 Ma), and ECM likely evolved in the Jurassic to Middle Cretaceous 200–100 Ma (Cairney 2000). The type of mycorrhizal association has implications not only for NPP but also for ecosystem nutrient cycling (Phillips et al. 2013). Mycorrhizal types are also associated with plant functional syndromes that differ in carbon economies and nutrient dynamics. For example, EM and ECM fungi have saprotrophic capabilities that enable them to access organic forms of nutrients that are not accessible to AM fungi (Read 1991). Plant species associated with ericoid and ectomycorrhizal fungi generally produce leaf litter that decomposes slowly relative to plant species associated with AM fungi, slowing down rates of carbon and nutrient cycling and leading to accumulation of soil organic horizons (Cornelissen et al. 2001, Phillips et al. 2013).

Symbiotic bacterial nitrogen fixation transformed the Earth's biogeochemistry starting in the Cretaceous. The predisposition to evolve symbioses between angiosperms and their N_2-fixing bacterial symbionts appears to have evolved once ca. 110 Ma (Werner et al. 2014). The origin can be pinpointed within the flowering plant clade of core eudicots at the common ancestor of four orders (Fabales, Rosales, Cucurbitales, Fagales), subsequently leading to eight or so origins within this broad clade, including the evolution of distinct symbiosis types (rhizobial bacteria and actinorhizal *Frankia* spp.). The ability to nodulate has been lost at least 10 times, including multiple times within the legumes. Legumes and other lineages within the nitrogen-fixing clade are now present (in varying abundance) in nearly every biome on earth. Because of the relatively high rates of nitrogen fixation achieved by symbiotic nitrogen-fixing legumes and actinorhizal species, symbiotic biological nitrogen fixation dominates nitrogen inputs to land ecosystems (Vitousek et al. 2013). Increased nitrogen inputs associated with the evolution of this clade may have been an important requirement for the evolution of broad-leaved species with high foliar nitrogen concentrations, rapid photosynthetic rates, and rapid leaf turnover rates, characteristic of the fast end of the leaf economic spectrum.

Other evolutionary innovations associated with nutrient acquisition include cluster roots, proteoid roots (Proteaceae and Fabaceae), dauciform roots (Cyperaceae), and capillaroid roots (Restionaceae), all of which provide advantages in low-phosphorus soil using similar mechanisms (Shane et al. 2006). The fossil evidence indicates the Proteaceae may have evolved 93 Ma and radiated after the breakup of Gondwana in the middle Eocene in Australia, South Africa, New Zealand, and Tasmania, where their ability to acquire phosphorus has proven advantageous in the low-phosphorus soils in parts of these regions. Cluster roots increase plant access to scarce water and nutrients, particularly phosphorus. They secrete organic acids that solubilize mineral-bound phosphorus and phosphatase enzymes that mobilize organically bound phosphorus (Lambers et al. 2008, Neumann & Martinoia 2002, Skene 2000). In South Africa and Australia, lineages with proteoid roots are restricted to highly weathered soils of extremely low fertility (Stock & Verboom 2012). Cluster roots, similar to the fungal and bacterial symbiotic associations discussed above, are important innovations for nutrient acquisition in plants that influence community assembly and ecosystem processes (Lambers et al. 2008).

In addition to these specific mechanisms, many species have evolved to survive in low-nutrient conditions by growing slowly and using nutrients conservatively (Chapin 1980). Insofar as growth rate and resource use can be assessed by knowledge of leaf traits such as leaf nitrogen and specific leaf area, conservative resource use appears to be characteristic of the Proteaceae, Ericaceae, and Acrogymnospermae, clades that also have root morphologies or mycorrhizal symbioses specialized for low-nutrient environments (Cornwell et al. 2014). By contrast, species with less conservative resource use are distributed across many clades. Thus, adaptation to very low-nutrient environments has a strong phylogenetic signal in terms of innovations in both nutrient acquisition and overall nutrient use.

Community Assembly: Biogeographic Affinities Drive Lineage Sorting and Ecological Differentiation Within Communities

The legacy effects of contrasting biogeographic origins often persist in the trait diversity of modern communities (Lechowicz 1984). Species sort along environmental gradients or display contrasting resource acquisition and use strategies, reflecting the legacy of the environmental context in which they evolved (**Supplemental Figure 3**). Co-occurring species can effectively occupy different environments, altering selection pressures and the suites of traits that promote survival. For example, plants with deep roots may access persistent water supplies, relaxing selection for drought-tolerant xylem and leaf physiology (e.g., Holbrook et al. 1995) compared with species with shallow roots. Coadapted suites of traits contribute to niche conservatism, as lineages sort into microhabitats (in space and time) best suited to their physiological strategies (Ackerly 2003).

As taxa shift from one biogeographic regime to another, perhaps along climatic gradients, adaptations to previous environments may only shift gradually even after their adaptive significance has waned. For example, *Salix* spp. from circumpolar origins have diversified, expanded their ranges, and now reach into Florida, Mexico, and tropical regions. Experimental tests reveal much greater freezing tolerances than required for their current distributions (Sakai 1970), though southern species have lost freezing tolerance relative to more northern species (Savage & Cavender-Bares 2013). Hysteresis can be seen as the shift in the relationship between freezing vulnerability and current temperatures in which the species live when lineages that evolved in circumpolar regions are compared with those that evolved in the tropics (Figure 1). Despite maintenance costs and trade-offs, the strength of selection to lose freezing tolerance may be lower than that to acquire it. In both lineages, persistence of suites of traits from their former regime may influence the microhabitats they occupy in modern communities.

Other important examples of local sorting in relation to biogeographic origins include the distribution of tropical versus temperate lineages along elevation gradients in Mexico (Graham 2011) and the restriction of temperate lineages in the southeastern United States to more mesic sites, including ravines, whereas subtropical taxa occupy dry sandy soils (Godfrey 1988). Among oaks (*Quercus*) in Florida, the northern deciduous species tend to occur in nutrient-rich mesic sites, whereas subtropical species tend to occur in scrub and sandhill habitats (Cavender-Bares et al. 2004). In the Pacific Northwest, mesic-adapted northern temperate herbaceous species and xeric-adapted species of subtropical ancestry sort along elevation and edaphic gradients within local communities (Harrison et al. 2010).

Sedio et al. (2013) showed that species within two genera (*Psychotria* and *Palicourea*) from a tropical clade of forest understory shrubs originating from distinct biogeographic regions in the Neotropics (South and Central America) occupy contrasting hydrologic habitats on Barro Colorado Island, Panama. Variation in hydraulic traits (leaf water potential at turgor loss point), which parallel the soil moisture microhabitats they currently occupy, is associated with the climates in the regions where their ancestors diversified. Ancestral climatic niches thus appear to drive species' habitat distributions millions of years after dispersal into new geographic regions. Trait optima from phylogenetic, comparative models reflect the contrasting origins of species within the clade and provide evidence of persistent niche conservatism even as the species intermingle in modern communities.

Within Mediterranean regions, clades also sort into microhabitats based on their origins (Stock & Verboom 2012). In the South African Cape flora, generally high-nutrient clades (*Asterales, Poaceae, Caryophyllales*) with high foliar nitrogen and phosphorus, and low nitrogen:phosphorus ratios, occur on more nutrient-rich granite-derived soils, whereas low-nutrient clades (Restionaceae, Ericales, Proteales) are restricted to nutrient-poor, sandstone-derived soils (Stock & Verboom 2012). Nutrient adaptations appear to persist within lineages even with transitions across climate zones. For example, as in South Africa, many Ericales in northern temperate or boreal systems are restricted to shallow, acidic, nutrient-poor soils on sandstone bedrock as well as nutrient-poor bogs.

In North American prairie grassland communities, biogeographic origins and niche conserva-tism are apparent in the community assembly and seasonal separation of cool season C_3 grasses [the Bambusoideae-Ehrharteae-Pooideae (BEP) clade] and warm season C_4 grasses [the Panicoideae-Arundinoideae-Chloridoideae-Micrairoideae-Aristidoideae-Danthonioideae (PACMAD) clade], irrespective of whether the species are native or introduced. C_3 grasses from the cold-tolerant BEP clade (Edwards et al. 2010) grow in the spring and early summer, taking advantage of cooler temperatures and moister conditions, whereas the C_4 grasses from the warm-adapted PACMAD clade (**Edwards et al. 2010**) begin growth later when temperatures are higher and water availability is often lower, maximizing growth in midsummer. Differences in climate-associated phenology promote resource partitioning and coexistence of these functionally contrasting lineages in grassland systems (**Fargione & Tilman 2005**).

BIOGEOGRAPHIC ORIGINS AND LEGACY EFFECTS ON TRAITS THAT DRIVE RESPONSES TO GLOBAL CHANGE

Biogeographic origins and lineage-based constraints are likely to influence the way plants respond to global change in the Anthropocene, including warming, changes in seasonality and rainfall, elevated CO_2, atmospheric nitrogen deposition, and disturbance, especially changing fire regimes. We generally expect species shaped by contrasting biogeographic histories to respond to resource limitations and environmental factors in contrasting ways. A general prediction is that taxa that have evolved under strong resource limitation will have evolved trade-offs that enhance persistence in low resource, stressful, or unstable environments at the expense of high performance in contrasting environments (**Chapin 1980**). Surprisingly, we know little about what to expect in response to some Anthropocene changes. To the extent that biogeographic history provides a predictive framework, it may provide guidance in managing ecosystems for the future.

Biogeographic Origin Diversity and Ecosystem Function

Studies of diversity and ecosystem function have emphasized the importance of functional diversity as a mechanism contributing to enhanced productivity and resilience (**Cadotte et al. 2012**). In some but not all systems, phylogenetic diversity is a stronger predictor of functional diversity, compared with species diversity alone, reflecting functional differences among clades. In this review, we have focused on the effects of biogeographic origins, as opposed to phylogeny per se. These effects may be strongly concordant in many cases, but as noted earlier, they are conceptually distinct and in some cases may be largely decoupled. As we have outlined above, lineages with contrasting biogeographic origins often partition resources or environmental gradients within communities. Thus, we believe that a diversity of biogeographic origins may be a strong predictor of functional diversity in both experimentally constructed and natural communities, contributing increased resilience in the face of global change.

Drought

Rising temperatures increase potential evapotranspiration and will likely make the world effectively drier in many places, independent of changes in rainfall. Additionally, climate models project that arid and semiarid midlatitudes are expected to become even drier than at present (**Collins et al. 2013**). Biogeographic origins are likely to influence which taxa are most vulnerable to drought. For example, in herbaceous communities of lowland montane forests in Oregon, where Robert Whittaker sampled vegetation from 1949 to 1951 at more than 400 sites, climate change has led to a 2°C warming and effectively drier climate since that time (Harrison et al. 2010). Subsequent vegetation surveys show that species change is linked to biogeographic history. Species of northern biogeographic affinity, those belonging to families or genera that were part of the mesic pantemperate Tertiary flora (Raven & Axelrod 1978), showed marked declines during a 60-year period. In contrast, during the same period at higher elevations, where cool, moist conditions have persisted, herbs of northern temperate biogeographic origins have modestly increased (Harrison et al. 2010). Other long-term data sets from areas that have experienced prolonged drought (e.g., California and the southwestern United States) may yield similar insights into the role of biogeographic origin as a predictor of changes in species abundances with drought.

Temperature

Consideration of recent biogeographic history and the innovations that may have arisen in response to changes in paleoenvironments may be informative in understanding the responses of organisms to warming temperatures. Because of the differential effects of temperature on photorespiration in C_3 and C_4 species, these alternative photosynthetic pathways will likely influence how grasses will shift their ranges in response to warming as climate changes. However, C_4 photosynthesis has evolved repeatedly in many lineages both within and beyond grasses that differ in their biogeographic origins and climatic adaptations (Edwards et al. 2010, Pau et al. 2013, Sage et al. 2011). Therefore, considering climatic origins and niche conservatism in addition to photosynthetic pathways is important for predicting the responses of species to climate change.

Dick et al. (2013) argued that Neotropical genera may persist as temperatures increase with climate change because these taxa are adapted to temperatures warmer than those experienced today. They documented that species are much older than previously assumed, dating back to the Pliocene (2.6–5 Ma) and Late Miocene (8–10 Ma), when air temperatures across Amazonia were similar to temperature projections for 2100, under low- and high-carbon emission scenarios, respectively. Their age estimates of Neotropical tree species provide a basis for predicting that these species will have a low risk of extirpation under future climate change, given that they evolved under warmer temperatures. However, species age may be less relevant than the strength of ancestral legacy effects, and we do not have a strong basis to predict the limits to these inherited environmental tolerances.

Atmospheric Chemistry: CO_2

Among the uncertainties in how biome responses to global change will feed back to accelerate or decelerate the pace of climate change is the magnitude of the CO_2 fertilization effect: enhanced carbon uptake induced by higher concentrations of atmospheric CO_2. Although soil fertility will constrain the magnitude of CO_2 enhancement on plant growth (Reich et al. 2014), species environmental history will also likely influence response to rising atmospheric [CO_2]. In particular, as explained above, because C_4 species already concentrate CO_2 intracellularly to accelerate photosynthesis, they are expected to show limited sensitivity to elevated atmospheric [CO_2] relative to C_3 species (Wang et al. 2011). This expectation suggests that elevated [CO_2] could place C_3 species at a competitive advantage. However, rising [CO_2] will occur concurrently with warming and, in some places, drying. Warming (under high light) can offset the competitive advantage conferred by elevated [CO_2] to C_3 species because of increased photorespiration (Collatz et al. 1998). Warming may thus favor C_4 species (Edwards et al. 2010, Still et al. 2014), even under elevated [CO_2]. C_4 species generally have higher WUE than C_3 species, as a consequence of lower stomatal conductance, and a higher WUE may offer advantages during drought. However, C_4 plants may become heat stressed under prolonged drought due to low stomatal conductance (Ghannoum 2009). This finding makes predictions of the abundances of C_4 and C_3 species under multiple global change factors difficult.

Seasonality and Photoperiod

Phenological differences likely will influence the vulnerability of plants to changing seasonality and increased variability in climate. Species differ in whether they respond to day length or temperature cues for leaf-out (Polgar & Primack 2011), complicating predictions of phenological responses to climate change, especially as species migrate poleward. Species originating from northerly climates also require exposure to a certain number of chilling days before leaf-out (Samish 1954). Consequently, photoperiod- and chilling-sensitive woody species may be unable to rapidly track climate warming. Experimental 16-hour day lengths under controlled conditions triggered willow species originating above 55°N to initiate extremely rapid growth, whereas willow species from below this latitude did not respond to longer day length (Savage & Cavender-Bares 2013). The response suggests that more northerly species use day length as a cue to trigger rapid summer growth. If these taxa can tolerate higher temperatures, they will be better suited to take advantage of high-latitude day lengths than new migrants.

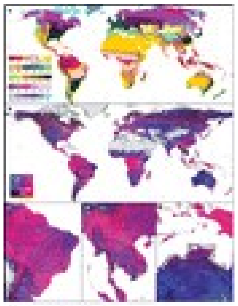
Mismatches between temperature sensitivities or tolerances and photoperiod are likely to impact growth and carbon uptake. Pau et al. (2011)proposed a phylogenetic framework for predicting how the phenology of species will respond to climate change. They hypothesized that species occupying higher latitudes or that are active early in the growing season should be most sensitive to climate change and have the most conserved phenological triggers. Species from aseasonal tropical environments might be less sensitive because phenology is likely to be less synchronized with climate. Within any given location, the biogeographic origins of species are likely to predict their phenological responses to changing climate, with species originating at higher latitudes leafing out earliest and fastest in response to spring warming. To the extent the biogeographic origins are consistent within lineages, phylogenetic information will be informative. However, for lineages that are broadly distributed across climatic gradients, it may be less useful.

Nutrients

Human activities—combustion of fossil fuels, production and use of nitrogen fertilizers, and cultivation of nitrogen-fixing crops—have increased inputs of nitrogen to terrestrial ecosystems through atmospheric deposition downwind of industrial and agricultural regions (Galloway et al. 2004). Plant communities are highly sensitive to increased nitrogen inputs, in terms of biomass, productivity, diversity, and species composition (Isbell et al. 2013, Stevens et al. 2015). Nitrogen enrichment increases the abundance of species that are poor competitors for nutrients but good light competitors (Helsen et al. 2014); these species have high foliar nitrogen concentrations (Diekmann & Falkengren-Grerup 2002). Studies examining the biogeographic origins of species that respond positively to nitrogen enrichment are limited, but certain lineages (Ericaceae, Fabaceae) appear to decrease, whereas others (Poaceae) increase (Helsen et al. 2014). Within the Poaceae, C_3 species are inclined to increase with nitrogen addition (Isbell et al. 2013). It is reasonable to hypothesize that lineages originating in or adapted to regions where nitrogen is abundant relative to other nutrients (phosphorus, potassium, calcium, etc.) might respond most positively to nitrogen enrichment in presently low-nitrogen regions. These lineages would include species from lower latitudes that have high phosphorus use efficiency (Hedin et al. 2009), low nitrogen use efficiency (Kerkhoff et al. 2006), and high nitrogen:phosphorus ratios (McGroddy et al. 2004, Reich & Oleksyn 2004).

USING BIOGEOGRAPHIC AND EVOLUTIONARY INFORMATION IN RESTORATION, MANAGEMENT PRIORITIES, AND ECOSYSTEM ENGINEERING IN A RAPIDLY CHANGING WORLD

This review has emphasized that current ecosystem function depends on legacies from the past. If we were to rerun the tape of life, different outcomes would be possible. Examination of regions where alternative plant and ecosystem functions have emerged against similar climatic backgrounds provides one approach to detect the signature of legacy effects. For example, with current technology and available or imminently available satellite data (Jetz et al. 2016), it will be possible to compare the functional trait distribution, composition, and variability of ecosystems globally with their climatic conditions and geologic settings (Figure 2). Many plant functional traits can now be remotely sensed using hyperspectral data (**Supplemental Table 1**). Integration of these new data with knowledge of species distributions should enable identification of regions where the same or highly similar climatic and geologic regimes support contrasting sets of functional traits and ecosystem functions. Human land use changes also leave important legacies that would need to be distinguished from evolutionary legacies, requiring coordination of satellite inference with ground observations and data on recent anthropogenic impacts. Improved knowledge of how plant performance and ecosystems are shaped by paleoenvironments provides guidance for understanding the importance of evolutionary legacy effects in current patterns of ecosystem function.



These same approaches can be used to help restore and manage ecosystems to meet human needs and objectives. Given myriad human-caused changes to climate, the atmosphere, and the cycling of elements, it is incumbent on humans to manage the Earth system at a global scale, and biologists will be increasingly called upon to help guide such efforts. Although conserving pristine ecosystems is a major conservation priority, demands for restoration, ecosystem engineering, and global landscaping (sensu Foley et al. 2011) are rapidly growing. Restoring systems to historical baseline conditions may be insufficient to maintain ecosystem function as we are increasingly confronted with novel environments and perturbations to which these systems are ill adapted. Historical assemblages are increasingly viewed as guides for restoration but not the end goals (Higgs et al. 2014), whereas desired functions are critical to sustain both biodiversity and ecosystem services. At the same time, our earlier discussion of contingent trait syndromes highlights that when taxa are selected in a restoration context for particular traits that confer ecosystem services we value, others may come along for the ride with unintended consequences. Recently proposed restoration approaches offer ways to incorporate functional trait information (Ostertag et al. 2015), historical data at a range of timescales from human disturbance to paleorecords (Barak et al. 2016), and phylogenetic information (Cavender-Bares & Cavender 2011, Hipp et al. 2015). In the face of rapid global change, it is legitimate to consider options designed for the purpose of fostering ecosystem functions and services, including system resilience and enhancement of evolutionary potential (Faith 2015, Forest et al. 2015), alongside conservation and management approaches that focus primarily on biodiversity and endangered communities.

Ostertag et al. (2015) proposed a five-step restoration approach that involves (*a*) establishing objectives and constraints for the system, (*b*) selecting appropriate functional traits, (*c*) determining the species pool from which to draw, (*d*) collecting trait data from this pool of species, and (*e*) analyzing data to choose species according to local objectives and constraints. Explicit consideration of changing environments and how paleoenvironments have influenced plant function can be included within this framework as a proactive means to ensure the necessary range of ecosystem functions are sustained in a dynamic world. We further emphasize the need to include the biogeographic histories of organisms in considering: (*a*) how they are likely to respond to global change, (*b*) where they are likely to fare well in the future, and (*c*) how their diversity (including functional, phylogenetic, and biogeographic origin) may contribute to resilience given fluctuating conditions. A restoration perspective that considers historical biogeographic processes to restore the Earth's ecosystem functions may now be critical (**Barak et al. 2016**).

We may have to relax the focus on native species and local genotypes as we increase emphasis on genetic diversity, evolutionary potential, and the taxa that provide critical ecosystem functions and services in the context of global change. This strategy would only be wise if it could be advanced without unintended consequences of novel introductions, particularly given the potential to introduce undesired traits coupled to the target traits as a consequence of evolutionary history. Humans have long managed agricultural and forest ecosystems for resource provisioning and aesthetic services with minimal regard to native versus exotic status. Long-cultivated species take on important cultural significance (**Mann 2005**), as do many naturalized species, such as *Hibiscus tiliaceus* and other species introduced by Polynesians and appreciated by indigenous cultures in Hawai'i (**Ostertag et al. 2015**). We tend to differentiate agricultural landscapes from natural landscapes in our willingness to manage for specific ecosystem services. However, a range of land uses, including parks, suburban and urban yards, highway borders, and so forth, may need to be considered in terms of how they can contribute to the ecosystem services necessary for sustaining life support systems. Consideration of the native versus non-native status of plants that provide our regulating services may ultimately be less important than understanding how their evolutionary and biogeographic origins shaped their functions and likely responses to change.

With rapid environmental change and considerable uncertainty regarding what is natural in any given location, initiatives and discussions concerning managed relocation have emerged in an effort to save taxa, and the genetic diversity of those taxa, from extinction in the face of climate change (**Javeline et al. 2015**, **Richardson et al. 2009**). Integrative perspectives that embrace the process of natural selection and consider the need for sufficient genetic diversity given the dynamic nature of the environment (**Broadhurst et al. 2008**) may be warranted.

Ecosystem management at global scales is no longer beyond consideration. The Global Biodiversity Observatory proposed by **Jetz et al. (2016)** calls for a satellite mission to retrieve continuous global measurements of functional biodiversity that are linked with in situ observations of diversity, composition, function, and species distribution to aid in the management of Earth's ecosystem functions. High-resolution global-scale remote sensing information to detect changes in, and opportunities for, improving ecosystem functions will become increasingly available, providing a path forward to link biogeographic and evolutionary history to ecosystem function and services across geographic scales.

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

Funding was provided by the National Science Foundation (NSF) and the National Aeronautics and Space Administration (NASA) to J.C.-B., S.H., and P.T. (DEB-1342872) and by NASA to P.T. (NNX08AN31G). Much of the research that shaped our thinking on this topic was done as part of the Cedar Creek NSF Long-Term Ecological Research program (DEB-1234162). We thank Robert Ricklefs, Erika Edwards, Joy Ward, Andy Ciurro, Aditya Singh, Cathleen Nguyen, Kent Cavender-Bares, Tracy Twine, Michael Donoghue, Becky Ostertag, Rebecca Montgomery, Daniel Stanton, Jose Meireles, Nick Deacon, and Paul Manos for insights, comments on earlier drafts of this manuscript, or technical assistance with figures.

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