

# The Deep Past Controls the Phylogenetic Structure of Present, Local Communities

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## Abstract

Coexisting species may be evolutionarily proximate or distant, resulting in phylogenetically poor or rich communities. This variation is often considered to result from present assembly processes. We argue that, under certain conditions, deep-past processes might control the phylogenetic diversity of communities. First, deep-past effects involve macroevolutionary processes, such as diversification rate, niche conservatism, or dispersal, in the lineages that constitute communities. Second, deep-past processes in the respective region or in the habitat type play a role, for instance, through age, area, stability, or connectivity. Third, the deep past may affect communities via trophic interactions (i.e., communities of enemies or mutualists or communities of hosts). We suggest that deep-past effects can be identified in local communities by measuring phylogenetic diversity in different species pools. We also show how community phylogenetic diversity results in positive or negative eco-evolutionary feedback, and we identify present-day conservation challenges that may profit from a deep-time perspective.

## 1. COMMUNITY PHYLOGENETICS: PRESENT-DAY PROCESSES ARE INSUFFICIENT

Local communities can consist of very closely or very distantly related species. We operationally define local communities as species assemblages in patches that are small enough for all species to be in direct contact or to share a common competitor, enemy, or mutualist. Such a patch might be defined as a locality spanning a small surface, a patch of a habitat type, coexisting species of the same trophic level, or a host individual. Strong relatedness among species within communities is mostly quantified as low phylogenetic diversity, when we measure the phylogenetic branch lengths separating coexisting species, whether all species pairs or more specifically pairs of the most closely or most distantly related species are measured (Webb et al. 2002). Community phylogenetic diversity across all coexisting pairs of species can vary from tens to several hundred millions of years in distance. It can be extremely low, for example, in areas of high levels of recent endemism with coexisting species belonging to the same clade (Anacker 2011). Phylogenetic diversity is extremely high when coexisting species belong to very distantly related clades, which can include old and/or relict species (Grandcolas & Trewick 2016).

Community phylogenetic structure has major ecological and evolutionary consequences (Cadotte & Davies 2016). Ecological consequences of the coexistence of close relatives include increased enemy pressure (Yguel et al. 2011, 2014) or increased establishment of alien species (Gerhold et al. 2011). Evolutionary consequences of such coexistence notably include hybridization, which may erode species boundaries (Weber & Strauss 2016). Conversely though, the coexistence of close relatives might reduce their vulnerability to environmental change, both currently and in the evolutionary past (Prinzing et al. 2017).

Phylogenetic distance among coexisting species is often considered to be the result of present assembly processes, such as abiotic filtering, or biotic competition and facilitation (Cavender-Bares et al. 2009). Coexistence of evolutionarily proximate species can result from abiotic assembly—in other words, filtering where a habitat promotes closely related species with similar traits that are advantageous in the habitat. Coexistence of evolutionarily distant species can arise from biotic assembly, notably negative interactions such as competition in which closely related species with similar trait values are outcompeted (Webb et al. 2002). Present assembly alone, however, is insufficient to explain the variation in phylogenetic distances among coexisting species (Weber & Strauss 2016). For example, Bennett et al. (2013) found no relationship of local phylogenetic diversity to competition intensity in vascular plants. Instead, increasing evidence shows that evolutionary and historical biogeographic processes are at least as important as local and contemporary processes in shaping phylogenetic structure of communities. Speciation and extinction influence the phylogenetic structure of bird and primate communities to a degree sufficient to reverse the influence of local assembly processes when compared with a null model (Pigot & Etienne 2015). Greater diversification in the Neotropics and Cenozoic extinctions in the Afrotropics have influenced phylogenetic structure of tropical rainforest communities across these continents (Carlucci et al. 2017).

We review how and under what conditions deep-past processes might control the phylogenetic distance among species coexisting in present communities. We assess recent empirical evidence on evolutionary and historical biogeographic processes that are known to shape contemporary phylogenetic structure of local communities in various organisms, or at least have the potential to do so, and we formulate new hypotheses.

## 2. SPECIES POOLS IN TIME AND SPACE

Phylogenetic diversity of local communities can be driven by the phylogenetic diversity of a species pool—in other words, the species that can potentially establish in a given local community. Species

pools can be defined differently, and the choice of definition is crucial. Most commonly, species available in the region surrounding the local community are used as a pool (regional species pool) (Lessard et al. 2012). However, we show in the next sections the importance of choosing an appropriate species pool for the relevant system under study, and we differentiate between species pools for certain lineages under study, regional species pools, habitat species pools, and pools of enemies/mutualists on a host.

Although species pools have an uncontroversial influence on the structure of local communities, species composition alone fails to reflect the similarity between the pool and actual communities at the level of higher-order clades. We therefore use the term lineage pool (Gerhold et al. 2015) to highlight that a species pool may consist of the closest relatives, though often different species. Two conditions must be met to trace the influence of deep-past processes on local present coexistence via the composition of lineage pools, as described in the following sections.

## 2.1. Condition 1: Consistency of Lineage Pools in Time

Lineage pools should remain relatively unchanged in time despite dramatic recent perturbations such as glaciations and human impact (DiMichele et al. 2004, Bartish et al. 2010). Paleontological studies have revealed persistence of plant and animal assemblages, both terrestrial and marine, over many million years (DiMichele et al. 2004), caused by environmental fidelity in at least some parts of phylogeny (Wiens et al. 2010).

## 2.2. Condition 2: Consistency of Lineage Pools in Space

Constraints imposed by lineage pools should not be overridden in space by local immigration or rapid local adaptation (Ricklefs & Schlüter 1993). Local immigration and adaptation events between spatially neighboring communities sampled from different lineage pools are possible but potentially less influential than within a lineage pool. For example, plant lineages in the Canary archipelago are more capable of dispersing and diversifying within a habitat lineage pool across different islands than between lineage pools of different habitat types on the same island (reviewed by Francisco-Ortega et al. 2001).

In many cases, both conditions are fulfilled, suggesting that deep-past processes have the potential to affect phylogenetic distance among species coexisting in present communities. Cases when these conditions may not be fulfilled include discontinuous areas in time and space. For example, discontinuity in time may be the case in early postglacial landscapes where habitat types are replaced within a region as a natural successional process following local warming (Reitalu et al. 2015).

# 3. UNDERSTANDING THE ACTORS AND THE SCENES

Deep-past processes involve actors (i.e., lineages) and scenes (i.e., regions, habitats, and trophic levels; see also the **Supplemental Appendix**). Giving the consistency of lineage pools in time and space (Section 2), we discuss how the phylogenetic structure of contemporary local communities may be influenced by macroevolutionary processes in the constituting lineages (Section 3.1), in the region surrounding the community (Section 3.2), in the habitat type the community belongs to (Section 3.3), and at the relevant trophic level (Section 3.4).

## 3.1. Deep-Past Actors: Lineages

The phylogenetic distances among species coexisting in present-day local communities can be low if their lineages have produced many species, species have overlapping geographic ranges, and

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**Supplemental Material >**

species have retained similar habitats (Moen et al. 2009, Rabosky 2009; see also the **Supplemental Appendix**).

**3.1.1. Diversification rates.** Diversification rates vary dramatically among lineages. For example, the single species in the genus *Amborella* is sister to a lineage containing more than 200,000 other angiosperm species. Species diversity in lineages may correlate to local coexistence (Prinzing et al. 2016), but how species from diverse and depauperate lineages combine into local communities varies with spatial scale and across regions in ways that defy simple description. Diversification rates are related to both speciation rates and extinction rates, and teasing out the two is not always easy (Ricklefs 2006).

**3.1.2. Speciation versus extinction.** Production of many species is promoted by particular traits (Ricklefs 2006, Rabosky 2009, Ebel et al. 2015). Specifically, these traits may increase (a) variation within species (short generation time, sexual reproduction), (b) chance of cleavage of this variance into isolated units (gene flow only across short distances, polyploidization), and (c) persistence of these isolates (increased, e.g., by vegetative reproduction) (Moen & Morlon 2014). Indeed, the accelerated diversification rate of several angiosperm clades is associated with the evolution of innovative key traits (Sanderson & Donoghue 1994, Crisp & Cook 2012). The importance of these traits has been tested across multiple lineages, and some are particularly prevalent. Reduced generation time often increases the rate of trait evolution and thus promotes diversification (May 1978). This diversification is commonly associated with smaller body size, in both plants and animals (May 1978, but see Sanderson & Donoghue 1994). Limited dispersal abilities, although potentially reducing fitness, can result in increased speciation. Entire species assemblages may be characterized by low dispersal, as is the case with Cape shrubland vegetation, which has a high proportion of myrmecochorous species (Bond & Slingsby 1983). Flightless insects, more common on windy islands, are often island endemics (Wagner & Liebherr 1992). Conversely, good dispersal suppresses speciation (Proches & Ramdhani 2013).

Extinction, in turn, is increased by traits decreasing (a) the survival rate of local populations, (b) the rate at which new local populations are established (because of, e.g., large body size, low mobility, or high specialization), and (c) the global range size and thereby the number of local populations (Davies et al. 2011).

**3.1.3. Communities after recent diversification.** Local case studies provide support for high diversification being responsible for the increased coexistence of close relatives. Neo-endemism—in other words, recent evolutionary radiations in multiple lineages (primarily leguminous trees)—is responsible for low phylogenetic diversity in Amazonian white-sand forests (Guevara et al. 2016). Rapid speciation events in herbaceous plant lineages (including legumes) have resulted in low phylogenetic diversity in communities of the Qinghai-Tibetan Plateau, Central Asia (Yan et al. 2013). The recently radiated lineages Restionaceae and Ericaceae have produced communities with low phylogenetic diversity in the Cape shrublands (Proches et al. 2006). Recent and rapid radiations in the genus *Eucalyptus* (Crisp et al. 2004) have resulted in low phylogenetic diversity in Australian subtropical rainforest communities (Kooyman et al. 2011).

Overall, we propose that genomic, population genetic, and life history factors that locally contribute to high speciation and low extinction ultimately contribute to the high diversification rates of some lineages, which in turn reduce the phylogenetic distances among coexisting lineage members. For instance, one possible reason we might find closely related species of willow growing together (Savage & Cavender-Bares 2012) is because there are so many willow species resulting from the deep-past capacity to form many new species by hybridization. Or, one possible reason

we might find some microbial communities comprising closely related species (Horner-Devine & Bohannan 2006) is because of the deep-past capacity of these species to avoid extinction by continuously establishing many new populations.

**3.1.4. Old lineage survival and community patterns.** The production of many species requires lineage diversification across long time spans, reflected by high clade age and promoted by particular traits (Qian 2014, Ricklefs & Jönsson 2014). Little doubt exists that major diversification events happened in today's dominant groups (e.g., mammals and angiosperms) soon after they emerged, resulting in multiple lineages from each coexisting today. For example, the signature of angiosperm diversification in the 120–100 Mya interval can still be picked up in node age histograms across diverse plant assemblages (Proches et al. 2006, Bartish et al. 2016). Often, older clades have decreased speciation rates (Ricklefs 2006, Moen & Morlon 2014).

**3.1.5. Dispersal and overlapping ranges.** Commonly, overlapping ranges result from dispersal, which is favored by particular traits. The range limits of marine bivalves are phylogenetically conservative, which leads to the overlapping ranges of closely related species (Roy et al. 2009) and hence can result in low phylogenetic diversity. In tetrapods, key traits such as large body size and the ability to fly have facilitated rapid global colonization in multiple lineages, meaning globally overlapping ranges (Proches & Ramdhani 2013). Zooming in to the fine scales relevant to community-level coexistence, dispersal is needed for species resulting from allopatric speciation to meet (Moen et al. 2009). In a minority of situations involving sympatric speciation, coexistence can happen from the start, and dispersal often results in only one of the species occurring elsewhere (Pour et al. 2017).

We therefore expect that the combination of speciation mode and dispersal capacity contributes to coexistence of close relatives. Specifically, such coexistence can result from a scenario of paleo-endemism in which ancestors diversified locally and descendants stayed in their ancestral locality owing to lack of dispersal. Alternatively, such coexistence of close relatives may result from speciation among geographically separated populations followed by later geographic overlap due to high dispersal.

**3.1.6. Phylogenetic conservatism of habitat use.** Closely related species occupying more similar habitat niches than distantly related species has been termed, among other things, niche conservatism (Wiens et al. 2010; see also Losos 2008 for criticism of the term). Usually, the occupation of similar habitats among lineage members means that they will coexist at the community level more often than expected by chance (Prinzing et al. 2017). This pattern has been noted in a variety of local assemblages occurring across regional (Proches et al. 2006) and even global (Prinzing et al. 2016) scales. However, in specific cases such as the invasion of unoccupied habitats, or climate change, species' responses to environmental conditions can lead to adaptive evolution (Ackerly 2003); thus, close relatives will diversify in habitat use.

Factors favoring phylogenetic signal versus diversification of traits have been extensively studied (Reich et al. 2003). Nevertheless, very few specific studies relate the phylogenetic signal versus diversification of niches within lineages to other traits of these lineages. Basically, three types of explanations exist: (a) because adaptation is not needed (Pour et al. 2017)—this may have to do with niche construction or phenotypic plasticity; (b) because adaptation is difficult (Crisp & Cook 2012) due to variation being constrained (genetic constraints, allometries, trade-offs, architectural constraints) (Futuyma 2010), nonselective (gene flow, neutral evolution), or lost due to specialization; or (c) because local adaptation is slower than species turnover, and so community assembly replaces adaptation (Ackerly 2003, Prinzing et al. 2017).

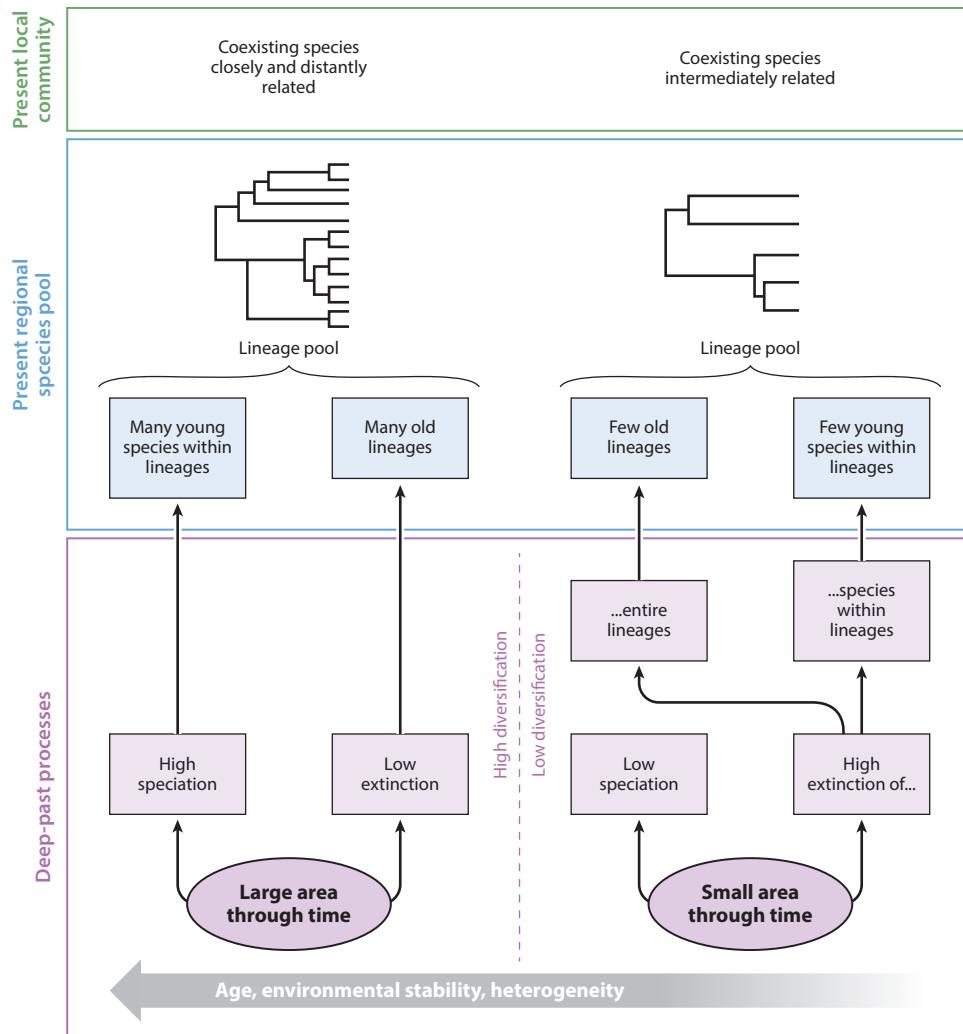
The various mechanisms outlined above should be more pertinent in some groups of species than in others. For example, large-bodied organisms can construct their own niche and pass it on to their descendants; modular organisms can exhibit plasticity; species lacking sexual reproduction may face genetic constraints; species with typically small population sizes will be subject to neutral evolution; and sorting may prevent adaptation in species with long generation times (Ackerly 2003, Reich et al. 2003, Losos 2008, Crisp & Cook 2012). We hypothesize that lineages in which such effects are relevant show stronger phylogenetic signal in niches; therefore, close relatives will encounter one another more often.

### 3.2. Deep-Past Scenes I: Regions Across Habitats

Biogeographic regions (hereafter referred to as regions) can exert major effects on present-day local communities, potentially overriding the importance of particular habitats or lineages (Ricklefs & Schlüter 1993). Regions are unique in the sense that they have idiosyncratic biogeographic histories. Specifically, age, area, environmental stability, environmental heterogeneity, and connectivity influence the origin, immigration, survival, and diversification of lineages. Therefore, the idiosyncratic deep-past history of a region affects the formation of regional species pools and their phylogenetic structures, thereby ultimately influencing the phylogenetic diversity of local communities assembled from the regional species pools.

Biogeographers often distinguish between museum and cradle regions or habitats (Mannion et al. 2014, Eiserhardt et al. 2017). The original concept stated that museums are communities preserving ancestral traits, whereas cradles are communities in which new adaptive traits evolve (Stebbins 1974). The museum and cradle concept has been used to investigate whether a region (e.g., the tropics) is diverse in species because it harbors many old lineages with ancestral traits due to low extinction (museum) or because it has high recent speciation rates with lineages carrying plenty of new adaptive traits (cradle). A region may be both a museum and a cradle (Mannion et al. 2014) by being a museum for some lineages and a cradle for others (Stebbins 1974, Eiserhardt et al. 2017). For instance, a tropical rainforest may be a museum for most lineages of woody plants that inhabit it, while it may be a cradle for lineages of epiphytic orchids constantly diversifying owing to their specialized interaction with pollinators (Stebbins 1974) (**Figure 1**). As a result, the regional species pool comprises both—many closely and many distantly related species. Although such a species pool produces the same average phylogenetic distance as a species pool comprising intermediately related species, the two phylogenetic structures may show very different geographical distributions (Davies & Buckley 2012) and consequences for ecosystem functioning (Yguel et al. 2016).

**3.2.1. Age, area, and stability of regions.** Regions vary substantially in age, area, and stability. A region may be as old as the Neotropics dating back to its separation from the Afrotropics ca. 110 Mya (Wilf et al. 2013) or as young as the Nearctic, where temperate conditions were mostly absent until ca. 30 Mya because the climate was very warm before the Oligocene (Latham & Ricklefs 1993). A region may be as large as the temperate forest zone in North America, which covers more than  $1.8 \times 10^6 \text{ km}^2$  (Latham & Ricklefs 1993), or as small as the Californian Mediterranean climatic region, which covers ca.  $7 \times 10^4 \text{ km}^2$  (Rejmánek et al. 1991). A region may be as stable as the Neotropics, where, in low latitudes and elevations, climate and vegetation have been typical of a tropical rainforest for at least the past 58 Myr (Wing et al. 2009), or as unstable as the boreal region, which is periodically subject to Milankovitch cycles (Fine 2015). The age of a region matters for both species and lineage richness of a regional pool (Wiens & Donoghue 2004) because speciation and extinction take time (Fine 2015). The effects of a region's age, area, and



**Figure 1**

Schematic depiction of two contrasting scenarios on how major biogeographic factors characterizing the history of regions affect diversification rates of lineages, thereby species pool formation, and ultimately phylogenetic distances among species coexisting in local communities. High availability of a large area through time and its correlates (age, environmental stability, and heterogeneity) drive major differences in diversification among regions. High speciation and low extinction in stable regions generate regional pools with many young species within lineages and many old lineages, respectively, which ultimately leads to high and low phylogenetic distances among coexisting species. In contrast, high extinction in unstable regions leads to few old lineages or few young species within lineages, which ultimately leads to intermediate phylogenetic distances among coexisting species.

stability on regional biogeographic history act synergistically according to the time-integrated area effect (Fine & Ree 2006, Fine 2015), which may be understood as the availability of area through time supported by regional stability. We may consider time-integrated area to be a leading factor explaining variation in lineage richness among regional pools because larger areas can harbor larger populations, which in turn increases speciation and decreases extinction probabilities (Fine 2015).

Moreover, stability can also lead to narrower niches related to tolerance to abiotic conditions and biotic interactions—in other words, higher specialization—all of which increases speciation rates (Fine 2015). Stability seems to have been particularly high and extinction low in southern Africa because Africa did not migrate across latitudes through the Cenozoic (although by then most of the continent had experienced high climatic instability) (Padayachee & Proches 2016).

Effects of high speciation and low extinction rates due to high availability of a large area through time (high stability) on lineage pools are twofold (**Figure 1**). First, high recent speciation leads to many young and closely related species within lineages in the regional pool. Second, low extinction rates over long time periods lead to many old lineages and distantly related species in the regional pool. The tropics may be an example of the effect of high availability and stability of a large area through time on phylogenetic distances. Most extant lineages of many groups of organisms (e.g., several angiosperm clades, New World birds) originated and persist in the tropics thereby conserving their tropical niches, because poleward biome shifts are hard and costly, as they would entail new adaptive traits related to tolerance to colder climatic conditions (Wiens & Donoghue 2004, Fine 2015).

In contrast, extinction plays a major role in unstable regions (**Figure 1**). Temperate and boreal zones may be examples of high extinction due to low availability of a large area through time (instability). Although temperate and boreal zones are large today, their availability through time has been short, owing to major glacial climatic oscillations during the late Cenozoic (Fine 2015). This low availability of area through time may explain the extinction of entire lineages. For instance, the extinction of entire lineages lacking cold tolerance during cooling times has been observed in temperate tree communities (Eiserhardt et al. 2015). Afrotropical rainforests also had low area availability owing to the unstable climate through the late Cenozoic, which led to extinction of species within lineages of palms and ultimately to intermediate phylogenetic diversity in local palm assemblages (Kissling et al. 2012). Therefore, high extinction in unstable regions (combined with moderate or low speciation) might lead to intermediate phylogenetic distances in regional species pools and ultimately in local communities. We note, however, that the outcome of high extinction rates depends on how extinction is distributed across the phylogeny, and the effect of instability on local phylogenetic diversity deserves further investigation.

**3.2.2. Environmental heterogeneity of regions.** A region may be as heterogeneous as the Neotropics, where there are tropical rainforests, montane forests with conifers, tropical wetlands, tropical montane herbaceous vegetation, savannas, tropical grasslands, temperate grasslands, and austral temperate forests, or as homogeneous as Greenland, where ice covers most of the landscape for most of the year and the vegetation is basically tundra and grasslands with small shrubs. An environmentally heterogeneous region may boost speciation (e.g., through parapatric speciation by generating spatial structure in the distribution of populations), which seems to be very important in the tropics (Fine 2015). Environmental heterogeneity might trigger sympatric speciation, in particular if part of the environmental space is not occupied, as may often be the case on islands [see research by Emerson & Gillespie (2008) on *Anolis* lizard assemblages in the Caribbean islands]. These speciation processes contribute to the presence of many young, closely related species within lineages in the regional pool in these examples (**Figure 1**). Conversely, heterogeneous regions may also promote refugia for old lineages. To survive climate changes, old lineages may track their conserved preferences for similar-to-old habitats across space through time (habitat tracking) (Ackerly 2003). High phylogenetic diversity in Andean tree communities seems to have resulted from the coexistence of old lineages (magnoliids) that have tracked Gondwanan-like habitats with recently derived lineages (eudicots) (Carlucci et al. 2017). Overall, environmental heterogeneity

of a region might produce species pools comprising both very closely and very distantly related species.

**3.2.3. Connectivity of regions.** A region may be well connected to other regions, such as Southeast Asia, which forms a corridor for migration of Palearctic and Australian taxa (Proches & Ramdhani 2013), or isolated from other regions, such as oceanic islands distant from continents. Connectivity may increase total area, thereby reducing extinction rates and promoting high phylogenetic diversity. Moreover, connectivity might promote high local phylogenetic diversity by creating biogeographic corridors for old lineages with conserved habitat preferences. The proximity of Southern Hemisphere continents during most of the Cenozoic might have enabled Gondwanan survivor lineages of angiosperms to migrate across continents (Kooyman et al. 2014). These Gondwanan survivor lineages are mostly conifers and ancient angiosperms (mostly magnoliids) with conserved preferences for shady, moist, and mild habitats (Kooyman et al. 2014). Such habitats are currently found at high elevations—for example, on the southern Brazilian plateau (Duarte et al. 2014) and in the Andes (Carlucci et al. 2017). In contrast, isolated regions may have been reached by fewer lineages and possibly triggered speciation, leading to low local phylogenetic diversity. Low phylogenetic diversity in the present-day assemblages of palms can be explained by deep-past geographic isolation and *in situ* speciation of the family (Kissling et al. 2012). Low present-day phylogenetic diversity in tropical reef fish faunas is associated with low connectivity of isolated refugia during the Quaternary (Leprieur et al. 2016).

### 3.3. Deep-Past Scenes II: Habitats Across Regions

Habitat types may be replicated across regions and carry consistent habitat lineage pools owing to a common deep-past history, which is largely independent of region (see also the **Supplemental Appendix**). The habitat lineage pools of grasslands on different continents resemble each other more than the respective regional lineage pools of a grassland and a forest on the same continent (Prinzing 2016). Some present habitat types have very ancient equivalents. Habitats seem to inherit diversification events from past epochs in which the equivalent habitat types were dominant. For example, contemporary dry habitats reflect diversification events of dry epochs in the deep past (Bartish et al. 2016). Certain habitat types have produced habitat lineage pools of evolutionarily proximate species, such as grasslands consisting of the clades of relatively recently radiated grass species (Strömberg 2011). Other habitats have produced habitat lineage pools of evolutionarily distant species—for example, by promoting the persistence of old lineages (Cornell 2013). We hypothesize that these habitat lineage pools influence the phylogenetic structure of the present-day communities assembled from the respective habitat, independent of the region.

Habitats may produce a pool of evolutionarily proximate species by various mechanisms, including (*a*) increasing speciation, decreasing within-lineage extinction, or increasing extinction of entire lineages; (*b*) preventing species within lineages from moving to other habitats and preventing species from other lineages from entering; or (*c*) facilitating the spread of species within lineages across the entire range of the habitat. We discuss below how these mechanisms may operate in conjunction with habitat attributes.

**3.3.1. Age of habitats.** Habitats can differ strongly in terms of age. Forests are generally much older than open habitat types such as grasslands: Tropical rainforests can be as old as 100 million years corresponding to the divergence of the first angiosperms (Morley 2000), whereas grassy growth forms developed during the Eocene, 56–34 Mya (Bredenkamp et al. 2002). Phylogenetic diversity can be high in old habitat types because old habitat types may have accumulated more

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### Supplemental Material >

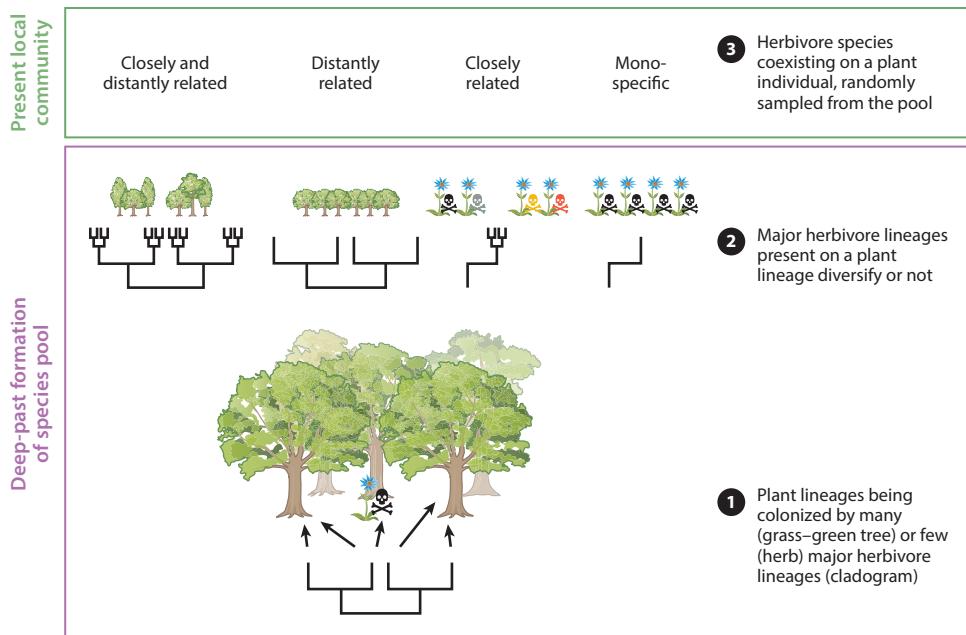
lineages that have been diversifying for a longer period. Proches et al. (2006) found that phylogenetic diversity of plant communities in South Africa was lower in evolutionarily young vegetation types such as in grasslands, when compared with old vegetation types such as subtropical thickets. This pattern was confirmed by Lososová et al. (2015) for species pools of vegetation types in Central Europe: Phylogenetic diversity was lower in young species pools of grasslands, open habitats, and human-made habitats from the Tertiary than it was in the old species pools of forests from the Cretaceous.

The question may arise as to why old habitat types have not been abundantly colonized by more recent lineages or young habitat types by more ancient lineages. This phenomenon may be the result of a home field advantage. According to this view, some major vascular plant lineages had established distinct ecological niches in a wide range of habitats, dominating over the lineages arriving later (Bateman et al. 1998).

**3.3.2. Size and isolation of habitats.** Habitats may be small and fragmented, such as stripes of sand dunes on sea shores, mountain tops, or ponds, or large and contiguous, such as the vast areas of rainforests or oceans. Large contiguous areas of tropical rainforest support larger populations and decrease the probability of extinctions (Fine & Ree 2006), resulting in high phylogenetic diversity. Small habitats forming isolated patches support small populations with low genetic variability, thus promoting habitat lineage pools of evolutionarily proximate species in different ways. First, small isolated habitats increase genetic drift favoring speciation over relatively short periods of time. Increased rates of genetic drift have been noted, for example, in the small isolated patches of alpine vegetation in New Zealand (Halloy & Mark 2003). Second, small isolated habitats may experience increased speciation due to empty niches. The extremely high speciation of *Lupinus* in the Andes has been associated with ecological opportunities afforded by the emergence of island-like habitats after the Andean uplift (Hughes & Eastwood 2006). Third, the long persistence of closely related species in isolation further promotes the creation and persistence of habitat lineage pools of evolutionarily proximate species.

**3.3.3. Stability of habitats.** Old-growth forests and natural grasslands are stable habitats, whereas successional, ephemeral, and anthropogenic habitats are unstable. Unstable habitats may promote dispersal and thereby gene flow, which in turn reduce genetic differentiation between populations. This reduction leads to low speciation rates and may end with the formation of habitat lineage pools of evolutionarily distant species. Marten et al. (2006) found lower genetic population differentiation in ephemeral habitats, such as lentic freshwater systems, than in stable habitats, such as lotic freshwater systems. In other cases, an unstable habitat may be inhabited by species with life history traits promoting success in such habitats. These traits include a short life cycle with many generations in a given time interval, which facilitates genetic recombination and mutations (Vamosi & Vamosi 2011). These factors may lead to high chances of speciation and the formation of a habitat lineage pool of evolutionarily proximate species.

Rarely disturbed habitats such as refugia increase the survival of local populations, thus lowering extinction rates and facilitating radiations, which promote the persistence of evolutionarily proximate species. Habitats in nonglaciated altitudinal zones have reduced extinction during glacial periods in several floras worldwide (Djamali et al. 2012). One refugium for forest chameleons in eastern Africa is dominated by a paleoendemic genus that has undergone no recent radiations yet has created a habitat lineage pool where phylogenetic diversity is lower than expected by chance (Tolley et al. 2011). Similarly, plant lineage pools of rainforest refugia in tropical Australia are rich in ancient lineages of Gondwanan affinity and have a lower phylogenetic diversity than predicted (Costion et al. 2015).



**Figure 2**

How the deep past explains why, on some hosts, enemies are closely related, using plants and herbivores as an example. (1) Some plant lineages may be colonized by many major herbivore lineages (*cladograms*), for instance, because they are large and apparent, abundant, and nontoxic and resemble other available plants. This is the case for the grass-green tree lineage, as opposed to the toxic herbs (*skulls*). (2) Diversification of these herbivore lineages on plants might then be fostered, for instance, by intraspecific variations among plants (*variations in tree shapes or skull colors*) or isolations among plant populations (*gaps between plants*). (3) Resulting present-day herbivore lineage pools consist of closely related species on some plant species, and of distantly related species on others, and so may be the herbivore communities sampled from these pools.

**3.3.4. Extreme habitats.** In some extreme habitats such as at high altitudes, random mutations induced by UV radiation may increase genetic variation (Willis et al. 2009; but see Bromham et al. 2015). High genetic variation increases speciation rates and may ultimately result in the formation of a habitat lineage pool of evolutionarily proximate species. Hot habitats such as those at low latitudes may select for species with short generation times, thus increasing genetic variation in populations and promoting speciation and habitat lineage pools of evolutionarily proximate species. The amount of solar energy affecting generation times and speciation is well-known as one of the explanations for high speciation rates leading to the latitudinal diversity gradient (Rohde 1992).

### 3.4. Deep-Past Scenes III: Trophic Interactions

The deep past may also affect the phylogenetic structure of contemporary communities via the trophic interactions in which species are engaged. This is true for local communities of enemies or mutualists on different host individuals (Figure 2) and for local communities of hosts interacting with enemies and mutualists. We develop both aspects in the following two subsections, mostly referring to plants as hosts.

**3.4.1. How the deep past explains why, on some host individuals, enemies or mutualists are closely related.** Enemies or mutualists using a given prey or host (hereafter referred to as host) may be phylogenetically very closely to very distantly related (Lewinsohn et al. 2005). Such relatedness patterns may result from present-day interactions (Webb et al. 2002). However, many host lineages have conserved characters through evolutionary time and hence have been tracked by a pool of enemy/mutualist lineages (e.g., Prinzing et al. 2017). Therefore, if a host species is currently used by a pool of closely related species, this might be because, in the evolutionary past, the host lineage was colonized by only a few major lineages of enemies/mutualists, each of which has produced many species, most of which survived (Janz & Nylin 2008) (**Figure 2**). Each of these three deep-past processes—colonization, speciation, and survival—might be favored by particular traits of the host lineages, and each might affect particular types of enemies or mutualists, as we discuss below. It remains to be tested whether today, on such host lineages, such mutualist or enemy lineages form pools of particularly closely related species and how this leads to relatedness within local enemy or mutualist communities on individual hosts.

Some characteristics of host lineages may have prevented the evolutionary colonization by most major lineages of enemies or mutualists, thereby potentially limiting the maximum evolutionary distances within the present pool of enemy or mutualist species available to colonize a host individual (**Figure 2**). First, some host lineages might be evolutionarily young—in other words, the host's characters are evolutionarily derived, such as those of grasses relative to those of pine trees. Few lineages of enemies or mutualists thus have had the time to evolve adaptations to these new host characters (Brooks & McLennan 2002), potentially explaining the association of old host lineages with old enemy lineages within some families of British plants (Ward et al. 2003). For other enemy or mutualist lineages, the time a host species has existed in a region might be more important than evolutionary age (Goßner et al. 2009). For instance, trees that have only recently arrived in Central Europe are colonized by few enemies (Brändle & Brandl 2001). Second, some host lineages might have been colonized by few enemy/mutualist lineages because these hosts are not apparent—in other words, they are encountered only rarely by potential enemies or mutualists (Feeny 1976), such as small herbs contrary to large trees (Winkler & Mitter 2008). This effect should especially limit colonization by enemies that are poor in tracking hosts, such as chewing, as opposed to galling, insects (Yguel et al. 2011, 2014). Third, some host lineages might have been colonized by only a few enemy or mutualist lineages because these hosts require specific adaptations, traded off against adaptations to other hosts (Agrawal 2000). The need for costly adaptation might be particularly strong (*a*) in host lineages with qualitative defenses, in other words, substances that directly harm the enemy, forcing enemies to develop major metabolic pathways of detoxification just to start colonizing such qualitatively defended hosts (e.g., *Asclepias*) (Mitter & Brooks 1983), though once successful, they may have undergone major diversification (Ehrlich & Raven 1964); or (*b*) in hosts that are the single representative of their lineage in a region and hence do not resemble the other hosts present (Connor et al. 1980).

Other host characteristics may have triggered speciation within the enemy or mutualist lineages that have succeeded in colonizing the host lineage, thereby potentially reducing the evolutionary distances within the present pool of enemy or mutualist species available to colonize a host individual (**Figure 2**). First, speciation can be favored by variable environments triggering differentiation by specialization. Some host species may offer more variable environments than others—either within or among host individuals. Within host individuals, a tree may have more structural or chemical variation than an herb, possibly explaining the strong diversification of herbivores on trees compared with herbs (Ward & Spalding 1993). Among host individuals, genetic variation is often high within tree species, potentially explaining the high diversification of the corresponding herbivore lineages (Whitham et al. 2003). Also, host species covering a wide range expose

their colonizers to wide environmental variation, potentially triggering speciation (Thompson et al. 2004). Second, speciation can be favored by cleavage among populations within an enemy or mutualist species. Such cleavage may occur if hosts form isolated populations, for example, during glacial–interglacial expansions and retreats (Nyman et al. 2012), or if hosts undergo evolutionary radiation (Ehrlich & Raven 1964, Farrell et al. 1991), notably in specialized enemies such as internal plant feeders (Janz & Nylin 2008). Cleavage may also occur if enemies/mutualists locally coevolve with hosts across a geographic mosaic (Thompson 2005). Cleavage among enemy or mutualist populations might even occur among different host individuals (Mopper 1996), in particular if enemies/mutualists are transmitted vertically such as in many parasites and symbionts (Winkler & Mitter 2008) or in herbivores that have a sessile gender or strong host fidelity such as scale insects or miners (Mopper 1996).

Finally, some host characteristics from a given host lineage may have ensured the survival of species that have been produced within an enemy or mutualist lineage, thereby further reducing evolutionary distances within the present pool of enemy or mutualist species available to colonize a host individual. First, species survive if their local populations survive. Local populations of enemies/mutualists are more likely to survive if their host individuals or host populations are large, long-lived, and continuously provide resources. Among plants, trees may live for centuries, and consistently, tree species tend to have particularly large numbers of herbivore species (Ward & Spalding 1993). However, for pollinators, even trees might provide only short-lived and ephemeral resources. Southeast Asian dipterocarp species, for instance, flower irregularly at intervals of many years and indeed harbor hardly any specialist pollinator species (Appanah 1993). In mutualists, local populations are more likely to survive if the host is capable of selectively favoring them and rejecting cheaters, as seems to be the case of mycorrhizal mutualists on plant hosts (Kiers et al. 2011). Second, enemy or mutualist species survive if many new local populations are formed. This is likely to happen if the hosts themselves often form new populations, as is the case in opportunistic ruderal plant species, though it remains to be tested whether enemies/mutualists sufficiently succeed in tracking emerging new host populations. Finally, species of enemies or mutualists survive if the total number of local populations is large, as will be the case in host species that are abundant and widespread. Consistent with this scenario, abundant and widespread host species often harbor numerous and rare species of enemies, suggesting low extinction rates (Brändle & Brandl 2001).

Together, these deep-past processes may limit the number of distantly related species and increase the number of closely related species within the present pool of enemy or mutualist species available to colonize a host individual (**Figure 2**). To our knowledge, no one has tested whether phylogenetic diversity on individual hosts can indeed be explained by these deep-past processes.

**3.4.2. How the deep past explains why closely related hosts may coexist.** During the deep past, different host or prey lineages have established interactions with different lineages of enemies or mutualists. For instance, most grasses are attacked by mammal herbivores and supported by arbuscular mycorrhizae, and most trees are attacked by lepidopteran herbivores and supported by ectomycorrhizae. Lineages of enemies and mutualists often differ in their degree of specialization. In this subsection, we argue that the enemies’ or mutualists’ level of specialization affects whether a host or prey should associate with closely or distantly related neighbors—in other words, whether the phylogenetic diversity of the host or prey community is low or high.

A plant host may interact with its neighbors via shared enemies. We argue that this interaction may push plants to associate with distantly related neighbors, notably if enemies are oligophagous and not limited by the defenses of surrounding hosts or by other external factors. It has long

been suggested that plants, by harboring host-specific herbivores, reduce the performance of conspecific or closely related neighbors (Janzen 1970, Yguel et al. 2011, Liu et al. 2012). Increased enemy pressure on hosts that are surrounded by phylogenetically closely related neighbors implies that enemies are oligophages rather than mono- or polyphagous—in other words, they can use several host species as long as they are closely related. Oligophages include many chewing insects, whereas monophages include many gall-forming or mining insects, and polyphages include slugs (Rathcke 1985, Winkler & Mitter 2008). Host species that are attacked by such oligophages should thus associate with distantly related neighbors to avoid being attacked by their neighbors' enemies. However, in particular cases, the opposite scenario can also be envisaged. If related host species share particular powerful defenses against their shared oligophagous enemies, a host might associate with closely related neighbors to profit from a shared enemy defense (Sotomayor & Lortie 2015). Moreover, association with closely related hosts might be advantageous if the number of enemies is limited by some external factors, such as mammal herbivores being limited by territoriality or top predators. In that case, the pressure from the limited number of enemies can be diluted among a large number of hosts (Deniau et al. 2018).

A plant host may interact with its neighbors also via shared mutualists. We argue that this interaction may push plants to associate with closely related neighbors, notably if mutualists are mobile and specialized. Some mutualists have specialized on particular host lineages, and some host lineages have developed specific rewards for their mutualists (Bascompte & Jordano 2007). A host surrounded by closely related neighbors might therefore recruit its neighbors' mutualists. For instance, many plants interact with specialized pollinators that are mobile and can be attracted across large distances to a patch of closely related species (Sargent et al. 2011). Conversely, other mutualist interactions might be much less specific, and the mutualists involved are of limited mobility. This seems to be the case at least for some mycorrhizal associations (Selosse et al. 2006). In such cases, it would be in a phylogenetically distant neighborhood that a given host might best recruit mutualists. These relationships possibly explain why distantly related plants host rather similar arbuscular endomycorrhizae (Veresoglou & Rillig 2014) and ectomycorrhizal enzymatic activity is higher on tree hosts in a distantly related neighborhood (Yguel et al. 2014).

Overall, if during the deep past, hosts associated with particular types of enemies or mutualists, this pattern might today push these hosts to associate with particularly closely related neighbors. Thereby, deep-past history may reduce the phylogenetic diversity of present-day host communities.

#### 4. CONCLUSIONS

Identifying the effects of the deep past on the phylogenetic diversity of a local community should start with measuring the phylogenetic diversity of different species pools, because deep-past processes definitely act on pools, whereas we often do not know to what degree they act on local communities. Comparing community phylogenetic diversity with the phylogenetic diversity of different pools, we can determine if, and which, deep-past effects have influenced a particular community. If community phylogenetic diversity does not correspond to the phylogenetic diversity of any of the pools, then we cannot say that deep-past processes are responsible for assembling the particular community.

Phylogenetic diversity should be measured for all pools: the pool of actors (lineages) and the pool of each scene (habitat type, region, trophic position). This process can be divided into three steps, each answering different questions.

1. Construct the pools. (a) A pool for the (dominant) lineages in a community can be constructed by randomly taking from the global phylogeny for a particular lineage the same

- number of species as found in a particular community. If the community's phylogenetic diversity does not significantly differ from that of the pool, community assembly has in all likelihood been influenced by deep-past processes in this dominant lineage. (b) A regional species pool can be compiled from available species lists in the region. Databases can help—for example, the Global Index of Vegetation-Plot Databases (<http://www.givd.info/>), sPlot ([https://www.idiv.de/de/sdiv/arbeitsgruppen/wg\\_pool/splot.html](https://www.idiv.de/de/sdiv/arbeitsgruppen/wg_pool/splot.html)), and Botanical Information and Ecology Network (<http://bien.nceas.ucsb.edu/bien/>) for plants. (c) As for a regional pool, a pool for a habitat can be compiled from species lists by categorizing the lists of sample plots or communities into habitat types. (d) Depending on the trophic position of the studied community, compile a pool of enemies/mutualists on a particular host (or hosts) for particular enemies/mutualists. A database is available for insects on food plants from the Biological Records Centre (<http://www.brc.ac.uk/dbif/>), although analyses of such databases may need to account for different sampling efforts on different host plants.
2. Compare the phylogenetic diversity of different pools with the phylogenetic diversity of local communities, and see which pool has the dominant influence on the particular community under study. For example, is the forest habitat type more important than the dominance of a certain lineage in such a forest community?
  3. Why do particular pools influence phylogenetic diversity of a local community? In the case of a dominant lineage, one should look at the diversification rate, niche conservation, age, and dispersal capacity of the lineage. In cases for which habitat has a major influence on the phylogenetic diversity of a local community, does the effect arise from habitat age, size, stability, isolation, etc.? At this stage, although data are available for some parameters, such as habitat age in particular vegetation types (e.g., Jacobs et al. 1999 for grass-dominated ecosystems), it may be more difficult to find data for other parameters.

## 5. OUTLOOK

### 5.1. Identifying Hierarchies of Deep-Past Impacts

We have identified deep-past impacts on community phylogenetic diversity operating at different levels: deep-past actors (lineages) and three types of deep-past scenes (regions, habitat types, trophic partners). These impacts trigger several questions: Is there a hierarchy among these four levels of deep-past effects on community phylogenetic diversity, and what are the underlying mechanisms? If it exists, what determines such a hierarchy? For example, under which circumstances do the effects of actors override the effects of scenes, and vice versa? When and where do deep-past regional effects dominate over deep-past habitat effects and trophic effects? At a finer level, we might ask: Is there a hierarchy among the different traits of actors (e.g., diversification rate, dispersal capacity of lineages) or of a type of scene (e.g., habitat age, habitat area, habitat stability) on community phylogenetic diversity? What are the underlying mechanisms? It would be interesting to test if different combinations of parameters lead to similar community phylogenetic diversity—for example, in old (triggering high phylogenetic diversity) and small (low phylogenetic diversity) habitats, when compared with young (low phylogenetic diversity) and large (high phylogenetic diversity) habitats.

### 5.2. Identifying Eco-Evolutionary Feedback

Deep-past processes may create species pools that are composed of phylogenetically distant species due to the survival of major lineages or of closely related species due to high diversification of

lineages into species that retain their ancestral niches. Communities sampled from these pools may reflect this species pool structure—in other words, coexisting species might be distantly or closely related, or both. Such coexistence may result in feedback on lineage survival, diversification, and conservation of niches. Feedback might be positive or negative. For instance, positive feedback would occur if coexisting closely related species produce new hybrid species (without the collapse of the parent species) or exchange mutualists, thus rarely going extinct and retaining their ancestral niche. In this case, recent diversification and niche conservatism would produce coexistence of close relatives, and this coexistence contributes to diversification and retaining the ancestral niche (Prinzing et al. 2017). In other scenarios, feedback might be negative—for instance, if hybridization collapses species boundaries or close relatives exclude each other through competition or exchange of enemies. Such feedback loops might possibly explain why some lineages or biota in some habitats, regions, or hosts become megadiverse and others impoverished.

### 5.3. Identifying Conservation Challenges

Although phylogenetic diversity and phylogenetic endemism have become important features toward novel conservation planning efforts (Pollock et al. 2017), they often act as black boxes summing up too many deep-time processes indiscriminately. It may be useful here to review a few of the processes relevant to deep-time-minded conservation.

Lineage pools are changing regionally through the introduction of non-native species, often from regions with completely different profiles in terms of ancient lineage survival and diversification, when compared with the regions of introduction. One example that has received ample attention in the literature is that of invasions to and from Australia and New Zealand. The introduction of mammals (belonging to cosmopolitan lineages) to previously (almost) mammal-free New Zealand is threatening endemic herpetofaunal lineages of truly great antiquity such as *Leiopelma* and *Sphenodon* (Proches et al. 2015). Conversely, transferring lineages that had diversified in isolation within Australia/New Zealand to other continents can now threaten native lineages and habitats as in the cases of *Acacia* and *Eucalyptus* (Richardson & Rejmánek 2011).

In a separate, yet interconnected way, anthropogenic habitat fragmentation means that, depending on organisms' dispersal abilities, regional pools may matter less at the local scale (see Butaye et al. 2002). Lineage coexistence is no doubt further affected by other anthropogenic impacts, such as the depletion of keystone lineages, filtering via modified abiotic factors, etc. It becomes evident from this enumeration that conservation and management efforts in our rapidly changing world could benefit from understanding when generalization is possible by considering the relevant region or the relevant habitat type and, indeed, when generalization is of little value. Such scenario planning is best informed by a broad framework for lineage coexistence and an in-depth knowledge of the main lineages involved.

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The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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