

Ecological and evolutionary perspectives on community assembly

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Ecologists often view community assembly as a process involving the dispersal of species from a static regional species pool followed by environmental filtering to establish the local community. This conceptual framework ignores the dynamic nature of species pools and fails to recognize that communities are assembled by processes operating over a vast range of temporal and spatial scales. Species pool richness and composition are influenced by metacommunity dynamics over short timescales and by speciation, extinction, and dispersal over long timescales. We suggest that a stronger focus on the geography of speciation, the formation of secondary sympatry, and the feedback between local and regional processes is needed to fully understand community assembly and the importance of dynamic species pools.

Species pools and community assembly

The richness and composition of biological communities (see [Glossary](#)) vary dramatically in time and space and the causes of this variation have been the subject of ecological research for decades [1]. The assembly of communities is often viewed as a process involving the dispersal of species from a regional pool and filtering by the abiotic and biotic environment to determine which species successfully colonize and coexist at a local site ([Figure 1A](#)). This basic conceptual model of community assembly is found in the theory of island biogeography [2], in the neutral theory of biodiversity [3], in some models of metacommunities [4], and in the general framework of modern species coexistence theory [5]. Largely ignored in each of these conceptual frameworks, however, is the question of how ecological and evolutionary processes interact to generate regional species pools.

Standard ecological models of community assembly treat the species pool as an independent entity that is immutable over the period of community assembly ([Figure 1A](#) and [Box 1](#)). This may be reasonable for some applications; for example, determining what ecological processes winnow out the species found in a local community from those that could potentially colonize a site. Such

applications typically take a null-model approach, focusing on comparisons of the observed species composition to that expected via a random draw of species found in the regional pool. Phylogenetic methods have been incorporated into these analyses to address the influence of evolutionary history and the phylogenetic signal of species traits in community assembly [6–9] and analytical tools have been developed to best tailor the definition of the species pool to particular applications [10–14]. However, as Pigot and Etienne [15] recently showed, applying phylogenetic relationships and null models to the study of community assembly can be misleading without recognition of the dynamic nature of species pools and the processes underlying species pool formation (e.g., allopatric speciation, dispersal, secondary sympatry).

Species pools are dynamic over a range of spatial and temporal scales. Metacommunity theory shows that species interactions within local communities and dispersal between local communities can be critical in determining the regional coexistence of species. Thus, metacommunity processes can influence the size and composition of the regional pool over short temporal scales and at small

Glossary

Adaptive radiation: the diversification by adaptation of a single phylogenetic lineage into multiple taxa occupying different ecological niches.

Allopatry: geographical separation between species.

Community: a group of species that co-occur in space and time and that have the potential to interact.

Community assembly: the process by which the species composition of a community is determined.

Ecological opportunity: the availability of unoccupied niche space, especially in species-poor communities.

Local scale: an area of relatively small spatial extent (i.e., less than a square meter to a few square kilometers) determined in part by the size of the organisms of interest (e.g., microbes, elephants). Within a local area, species have a high probability of encountering each other and may influence each other's dynamics.

Mass effect: the immigration of individuals into a community in a way that influences the recipient community's dynamics.

Regional scale: an area of relatively large spatial extent covering many square kilometers and containing a large number of habitats and communities. Functionally defined as an area in which the processes of speciation and extinction operate to affect biodiversity.

Secondary sympatry: the reestablishment of overlap in species ranges after allopatric speciation.

Speciation: the formation of two or more reproductively isolated species from an ancestral species.

Species pool: the set of species that could potentially colonize a local site or community over ecological time.

Species richness: the number of species present in a community or region.

Sympatry: geographical overlap between species.

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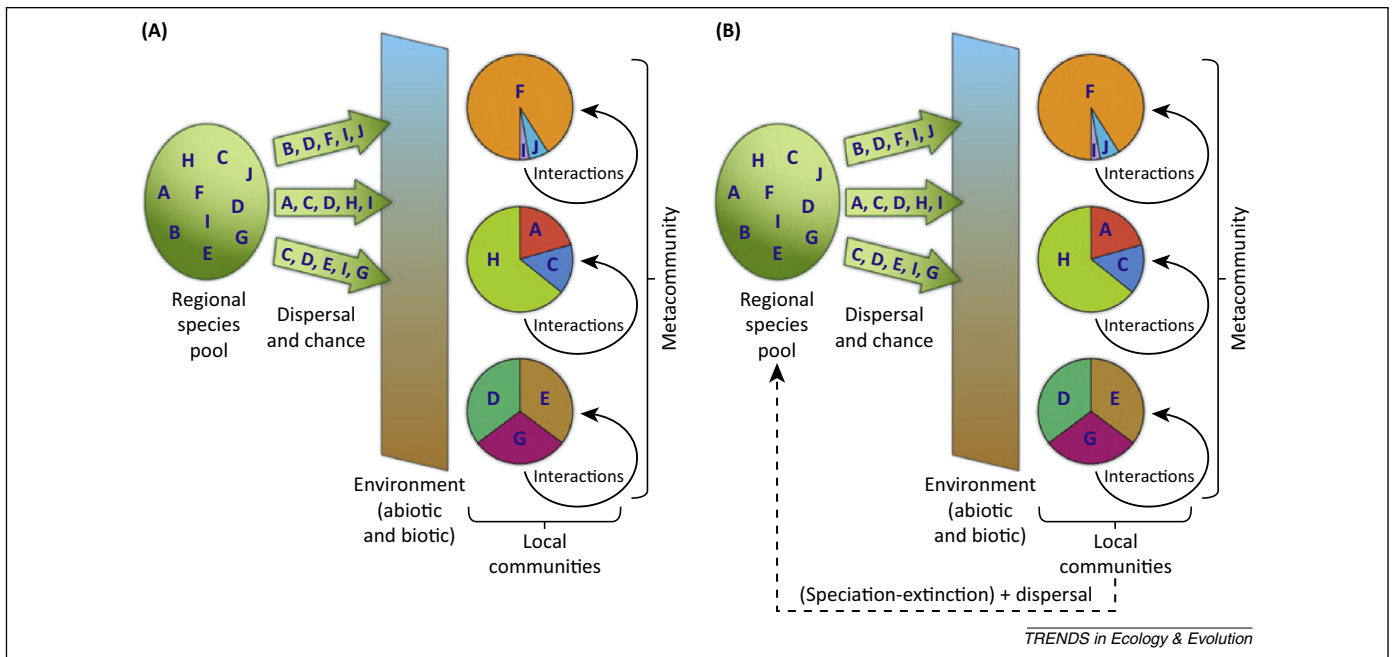


Figure 1. Two models of community assembly. **(A)** Local communities comprise a subset of species from the regional species pool that have passed through environmental filters. There is no feedback from the metacommunity (collection of local communities) to the regional species pool. Adapted from [5]. **(B)** Local communities are assembled as in (A), but speciation adds new species to the pool, extinction removes others, and dispersal allows the persistence of species that might otherwise go extinct.

spatial scales (Box 1). Moreover, to understand how species pools are generated over much longer time periods and across broad geographical extents (i.e., biogeographical species pools, *sensu* Carstensen *et al.* [13]), we require an understanding of the processes of speciation, extinction, and dispersal. Thus, we suggest that ecological and evolutionary feedbacks between local communities and the species pool (Figure 1B) deserve much more attention than they have received traditionally. Ecologists have largely sidestepped critical evolutionary mechanisms involved in the origin of the species pool, while evolutionary biologists have given scant attention to the relationship between the origin of species and the origin of community diversity. Our goal here is to highlight the feedback occurring between ecological and evolutionary processes that generate species pools, focusing first on well-studied island systems and then moving to larger continental scales.

Speciation and community assembly in island-like systems

The interplay between ecology and evolution in generating species diversity is readily seen in classic examples of adaptive radiations in 'island-like' systems such as Darwin's finches, *Anolis* lizards in the Greater Antilles, Hawaiian silverswords, and cichlid fishes in African lakes, where a relatively unoccupied environment is colonized by one or a few ancestral species. The theory of adaptive radiation proposes that competition for resources drives ecological divergence in niches, the diversification of forms, and, ultimately (with reproductive isolation), the formation of new species [16,17]. Moreover, it is hypothesized that, as the diversity of competing species increases, ecological opportunity (niche availability) declines and the pace of diversification slows [16,18–20].

Studies of adaptive radiation in island-like systems have yielded important insights into the ecological and evolutionary mechanisms generating biological diversity [21,22]. First, speciation is rare on small islands (unless they are part of a larger archipelago [23]). Below a minimum island size there is insufficient opportunity for geographical isolation, which suggests that allopatry is generally required for speciation. Second, niche filling on isolated islands above the minimum size for allopatric divergence is achieved by *in situ* speciation but niche filling on islands and archipelagos near the mainland is a result of colonization [24]. Third, morphological diversification within a single lineage (e.g., Hawaiian honeycreepers and silverswords) can occasionally rival the morphological variation (and functions) seen among phylogenetically distinct groups on the mainland. However, other seemingly similar taxa colonizing the island group may show little or no *in situ* diversification [21]. Thus, some clades diversify while others do not [25].

Finally, adaptive radiations may result in replicated radiation in which morphologically and ecologically similar species are produced independently, suggesting that niche filling has a deterministic component. Arguably the best documented example of convergent evolution involves *Anolis* lizards on the islands of Cuba, Hispaniola, Puerto Rico, and Jamaica [19,26,27]. On each of these islands, anoles have independently evolved a similar set of habitat specialists (ecomorphs), and Mahler *et al.* [26] showed that these replicated island radiations share the same adaptive peaks. Interestingly, however, bigger islands have more ecomorphs, suggesting that the degree of niche filling depends on the properties of the island (e.g., area, habitat diversity). Similarly, studies of adaptive radiation in cichlid fishes of African lakes [25,28] show that the propensity of lineages to radiate depends on environmental

Box 1. The application of species pools in ecology

The concept of the species pool was introduced to ecology more than a half century ago (e.g., [51–53]). Elton and others proposed that communities comprise a subset of the species that could potentially disperse to and colonize a site – the latter being defined as the species pool or source pool. Elton's idea of 'limited membership' (driven primarily by interspecific competition within a community) was challenged in the mid-1970s by demands for more stringent tests of nonrandom community assembly (e.g., [54]). Comparisons between realized community composition and expectations based on a 'null model' constituted the first application of the species pool concept to ecology [13,55]. Recently, phylogenetic relationships have been incorporated into this framework to assess the contributions of habitat filtering and species interactions to community assembly (e.g., [7–9,15]).

A second application of the species pool concept to ecology compares the species richness of local communities with the richness of the regional species pool [56]. A linear relationship between regional species richness and local species richness was hypothesized to reflect a strong influence of regional diversity on local community composition, whereas a saturating (asymptotic) relationship between regional richness and local richness was hypothesized to demonstrate the importance of local processes (e.g., interspecific competition, niche filling). Shurin and Srivastava [57] and Harrison and Cornell [11] review the complexities involved in interpreting local-versus-regional richness relationships.

The above approaches assume that the species pool is independent of the communities contained in a region. By contrast, the metacommunity framework recognizes that regional diversity may be maintained by the dispersal of species between communities [4]. Species may coexist regionally via a competition–colonization trade-off [58–61] or may be maintained locally via mass effects [62,63]. In both cases, ecological processes act across local and regional scales to set species richness. Similarly, the composition of the species pool depends on evolutionary processes (adaptation, speciation, range expansion, and secondary sympatry) and on species interactions that occur within and between local communities. To date, relatively little attention has been focused on the feedback that occurs between local community species composition, biotic interactions, and the diversification processes that generate regional species pools.

opportunities (e.g., lake depth, energy available, lake age), lineage-specific traits (e.g., intensity of sexual selection), and the composition of the fish assemblage [29].

Do the lessons learned from 'islands' about adaptive radiation, niche filling, and the generation of species diversity apply to the construction of species pools on continents (i.e., biogeographical species pools [13])? Perhaps. For example, Hughes and Eastwood [30] documented rapid and extensive adaptive radiation in the plant genus *Lupinus* in the Andes of South America (~85 species and a variety of life forms). They suggest that this is an island-like adaptive radiation played out on a continental scale and propose 'that lupine diversification was driven by ecological opportunities similar to those on islands created by the emergence of largely unoccupied habitats after Andean uplift and subsequent Pleistocene glaciation' ([30], see p. 10337). Similarly, the radiation of *Anolis* lizards in the Caribbean is mirrored by an extensive adaptive radiation in mainland Central and South America [17,31]. Although much less is known about the mainland radiation of *Anolis*, it appears that rates of evolutionary change and morphological diversity on the mainland may be similar to those on islands [31].

However, the process of diversification and the formation of species pools on continents (which often have relatively

old and stable environments) may differ from adaptive radiation on islands. For example, most island radiations involve diversification of one or a few clades in relative isolation from other potential competitors or predators. By contrast, continental radiation often involves a complex set of biotic interactions. For example, on the South American mainland, *Anolis* lizards compete for food with various birds, mammals, and frogs and are prey to many taxa that are absent on islands, which may be the cause of differences in morphology and habitat use between mainland and island anoles [17,31]. In addition, clades radiating on islands tend to remain endemic to the island systems in which they evolved, so they do not truly become part of the regional species pool [21,28].

The process by which truly continental species pools are formed (e.g., trees of eastern North America, songbirds of Eurasia) differs from that of adaptive radiation in island-like systems in that lineage diversification on a continental scale often occurs in multiple clades, where members of a diversifying lineage may interact with suites of unrelated species across a broad landscape. Further, species arising in allopatry must achieve secondary sympatry (i.e., overlap in geographical range following speciation) to occupy the same species pool. If sister species remain allopatric, it seems unlikely that they would meet the criteria of being in the same species pool (i.e., members of a set of species that can potentially colonize a local site over ecological time). We suggest that achieving secondary sympatry is an important and potentially rate-limiting step in the evolution of regional species pools and in the building of community diversity. As Price *et al.* [32] note, competition (and other species interactions) may strongly influence the ability of species to achieve secondary sympatry, underscoring the need to consider the feedbacks that occur between communities and the species pool (Figure 1B).

Building a regional species pool

Understanding the evolutionary processes driving regional diversity must include specific consideration of the geography of speciation (Box 2). Relatively few studies have examined the mechanisms underlying the development of species pools at continental scales and most have focused on diversification in one or a few clades (as have most studies of adaptive radiation on islands). We examine a few of these continental examples below.

McPeck and Brown [33] used a comparative biogeographical and phylogenetic approach, coupled with experiments, to examine the diversification of *Enallagma* damselflies across eastern North America. They found that many species in this clade are the result of recent (Pleistocene) speciation and that many co-occurring species show little ecological differentiation or evidence for adaptive radiation. Instead, they suggest that speciation was driven by mate recognition that occurred in small, isolated populations formed as a result of glaciation [34,35]. Nevertheless, Rundell and Price [36] suggest that the time since divergence of the common, sympatric *Enallagma* was long enough to allow the evolution of (perhaps subtle) ecological mechanisms of coexistence.

Most speciation is allopatric and much of the work on speciation emphasizes the evolution of reproductive barriers

Box 2. Community assembly and the geography of speciation

A key issue in the study of speciation and its contribution to community assembly involves the role of geographical barriers. In allopatric speciation, a geographical barrier prevents gene flow between populations and reproductive isolation evolves as a byproduct of divergent natural selection. In sympatric speciation, there is no geographical isolation and barriers to gene flow evolve in sympatry, while in parapatric speciation strong divergent selection between neighboring populations leads to the accumulation of reproductive isolation despite gene flow. In sympatric and parapatric speciation, increased richness of the species pool via speciation is not constrained by dispersal barriers. However, most speciation is allopatric [37], and this presents a conundrum for the development of regional species pools and, ultimately, for community assembly.

As geographically isolated populations evolve, reproductive isolation and niche divergence both increase (see Figure 2A–D in main text), and taken together these factors should promote coexistence if secondary sympatry is achieved. However, as allopatric populations become reciprocally adapted to their local environments they are also less likely to successfully colonize the geographical range of their sister species. For example, range expansion and broad-scale coexistence in the narrowly sympatric sister species *Mimulus lewisii* and *Mimulus cardinalis* is limited by strong local adaptation [64,65]. Reproductive

isolation as a consequence of local adaptation (i.e., ‘ecogeographical’ isolation [66] or ‘immigrant inviability’ [67]) is an important mechanism of speciation [68] but, as far as we are aware, has not been recognized as an obstacle to the formation of species pools.

How do species that evolve in allopatry achieve secondary sympatry and under what conditions are they likely to coexist? Figure 2E–G in main text illustrates three different scenarios. First, coexistence following long-distance dispersal may be impeded by strong local adaptation and/or competitive exclusion (see Figure 2E in main text). Second, adaptation to habitats beyond the ancestral range may result in range expansion and secondary sympatry, with coexistence achieved through diminished local adaptation and strong niche divergence (see Figure 2F in main text). Finally, large-scale environmental change may cause range shifts that erase local adaptation to ancestral habitats, with coexistence achieved because of prior niche divergence (see Figure 2G in main text). Where secondary sympatry results in coexistence (see Figure 2F,G in main text), subsequent adaptation to reduce niche overlap (competitive displacement) or hybridization (reinforcement) is possible. A clearer understanding of the factors that influence secondary sympatry and species coexistence is needed to better link the concept of dynamic species pools to the assembly of local communities.

[37], with little consideration for how speciation contributes to diversity at different spatial scales. In strict allopatric speciation without further migration, there is no increase in the diversity of the local community. Range expansion and secondary sympatry are therefore critical issues in the generation of both local and regional diversity [32,38,39]. In McPeck’s [40] damselfly system, Pleistocene glaciation appears to have provided both the opportunity for allopatric speciation (via geographical isolation) and the opportunity for range expansion and secondary sympatry as watersheds were reconnected following the glacial retreat. We suggest that such broad-scale environmental changes (e.g., glaciation) may facilitate post-secondary contact between species following allopatric speciation, allowing the development of regional species pools (a point we return to below). Moreover, speciation with gene flow (i.e., parapatric or alloparapatric speciation) may be more common than once thought and the evolution of reinforcing mechanisms that increase pre-mating isolation may often allow species with strong but incomplete reproductive isolation to coexist (T.D. Price, personal communication).

The formation of regional species pools in songbirds is different from that of North American damselflies, with much slower rates of diversification due to slow rates of secondary sympatry and niche filling [39,41]. Under a model of allopatric (or parapatric) speciation, regional diversity increases when sister species are able to expand their ranges to become sympatric (Figure 2). Using geographical distributions and a molecular phylogeny for >400 recently diverged species of New World birds, Weir and Price [39] estimated that secondary sympatry generally requires millions of years to achieve. Moreover, the authors concluded that sympatry in sister pairs took almost twice as long to achieve at low than at high latitudes (3.2 My at the equator and 1.7 My at 60° N). They proposed three hypotheses that, individually or in concert, might explain this pattern: (i) barriers to sympatry in the tropics last longer than those at high latitudes; (ii) tropical bird species have reduced dispersal capacity; and (iii) range expansion into secondary sympatry is more difficult in the

tropics because of greater community saturation and stronger interspecific competition.

Price [41] used phylogenetic analysis and field studies to examine the roles of time and ecology in the continental radiation of Old World leaf warblers, a clade of about 60 species of small, insectivorous birds found in temperate habitats throughout continental Eurasia. He concluded that: (i) leaf warblers diversified via allopatric speciation about 11–12 My ago; (ii) sister species remained allopatric for long periods (generally more than 3 My) before achieving secondary sympatry; (iii) complete reproductive isolation evolved in allopatry well before secondary contact; and (iv) competition limited diversification rate by preventing range expansion and further rounds of allopatric speciation. Price ([41], see p. 1759) notes that ‘Generally missing from previous discussion on controls of range expansions – and by implication speciation rate – has been the role that closely related species play in limiting mutual expansions into each other’s range’.

Most studies of adaptive radiation have focused on diversification within clades, not within communities. Recently, Price *et al.* [32] expanded their studies to 350 breeding species representing multiple clades of Old World song birds in the eastern Himalayas. In a broad phylogenetic analysis, they found that average time to sympatry among pairs of close relatives was about 7 My, much longer than the typical time for birds to achieve reproductive isolation (~3 My). Rabosky and Matute [42] also found that the time to achieve reproductive isolation in individual lineages of birds and *Drosophila* was not closely associated with their rate of speciation based on phylogenetic analysis, suggesting that factors such as geographical range expansion may limit the effective rate of speciation. Thus, Price *et al.* [32] conclude that local species interactions, by limiting rates of range expansion, may ultimately determine the size of regional biotas (but see [43]). This work emphasizes that strong feedback may occur between species interactions (e.g., competition) in local communities and the development of the regional species pool (Figure 1B).

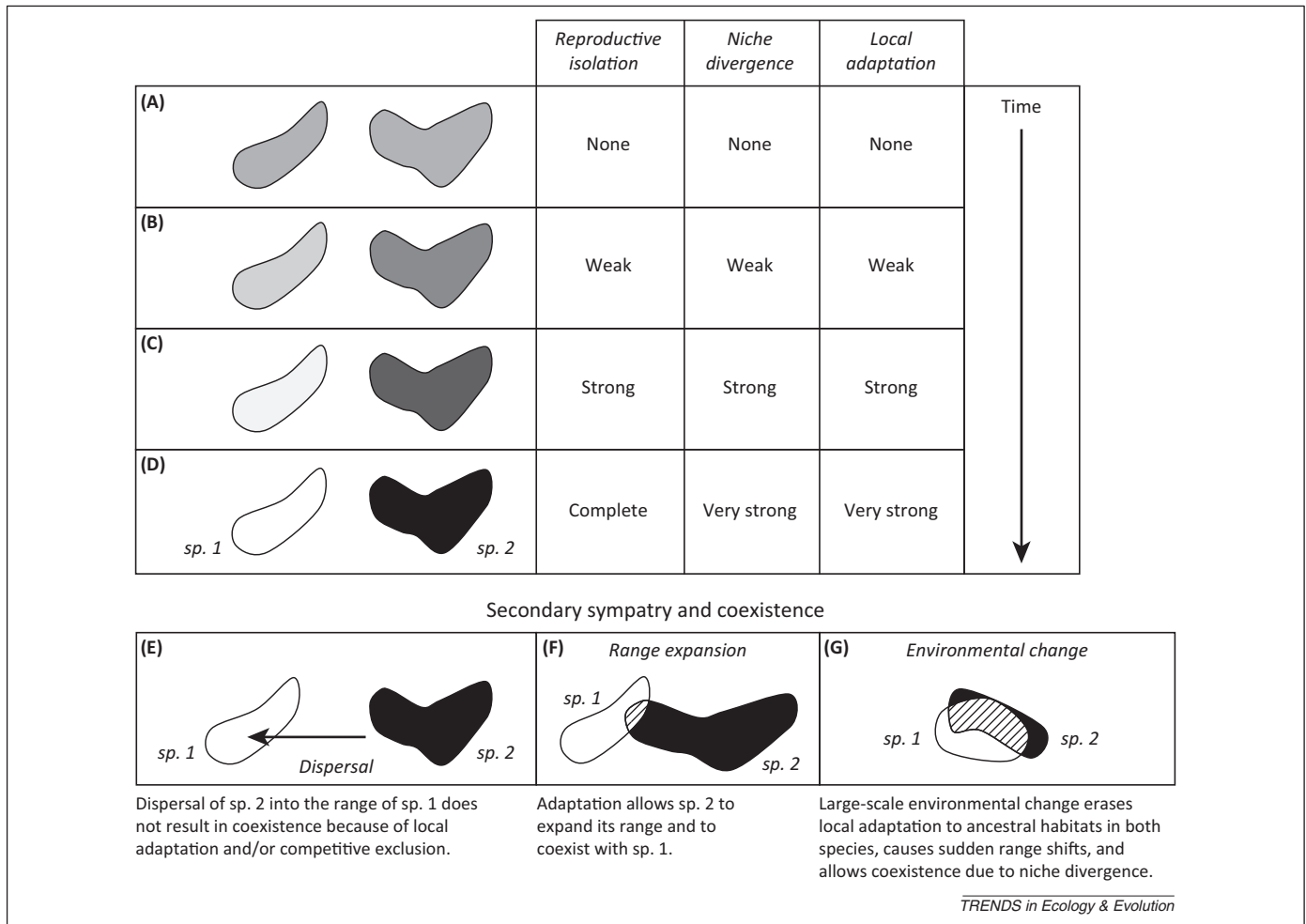


Figure 2. Consequences of allopatric speciation for community assembly. (A–D) illustrate the process whereby populations become geographically isolated (A) and evolve reproductive isolation (become separate species) as a byproduct of niche divergence and adaptation to their local environment (B–D). Three mechanisms of achieving secondary sympatry and the possible consequences for coexistence are depicted in (E–G): (E) dispersal of species 2 into the range of species 1 does not result in coexistence because of strong local adaptation and/or competitive exclusion; (F) adaptation allows species 2 to expand its range and to coexist with species 1 because of diminished local adaptation and strong niche divergence; and (G) large-scale environmental change causes range shifts that erase local adaptation to ancestral habitats and coexistence is achieved because of prior niche divergence. Scenarios (E–G) focus on mechanisms of stable coexistence between species and do not consider the possibility that species 1 and 2 may overlap in distribution but are undergoing slow competitive exclusion (i.e., neutral dynamics [3,33,35]).

Utility of the species pool concept for community assembly

How useful is the species pool concept for understanding the assembly of communities? The answer depends on the spatial and temporal scales of interest. Ecologists focused on understanding the processes governing community composition at local scales and without explicitly considering time for dispersal, adaptation, or speciation have reasonably employed the species pool concept to judge the relative importance of environmental filtering and biotic interactions (reviewed in [6,12,44]). By contrast, when considered over larger spatial scales and/or across evolutionary time, the utility of viewing the species pool as a static entity distinct from the factors that ultimately shape it (e.g., speciation, dispersal, species interactions) is problematic at best [15]. Community assembly occurs on various timescales, from the initial colonization of young, island-like habitats with few species to the accumulation of species in older, more diverse communities. Moreover, the relative importance of ecological versus evolutionary factors varies with temporal and spatial scale [45].

We suggest that the species pool concept has its greatest utility in the understanding of community assembly in young, island-like habitats with limited isolation and where ecological factors prevail or in assessing the strength of environmental filtering in the assembly of local communities (assuming a simple rain of propagules from an external pool over ecological time). However, even in these cases interpretations of community assembly based on environmental filtering can be problematic. For example, interpreting the under- or over-dispersion of phylogenetic distances in a community (compared with a random draw from the species pool) as evidence of environmental filtering or niche partitioning can be misleading without knowledge of the mechanisms promoting species coexistence [8] or without considering speciation dynamics in the formation of the species pool [15]. When we consider a time frame that allows adaptation and speciation, the ‘pool’ of species able to colonize a site becomes dynamic and community assembly depends increasingly on evolutionary processes that occur during allopatric speciation, such as divergent adaptation, the accumulation of reproductive

isolation, and the evolution of locally adapted populations, in addition to ecological factors that determine the potential for sister species to coexist (Figure 2).

Consider the value of the species pool concept in understanding community assembly on oceanic islands. The first stage of assembly in these habitats begins with colonization from the mainland species pool. Classic island biogeography theory (IBT), such as that espoused by MacArthur and Wilson [2], suggests that the number of species at equilibrium is a function of a declining rate of immigration of new species as island diversity increases and an increasing rate of extinction as species richness increases (as a result of smaller population sizes and a larger number of species that can go extinct). These dynamics are a product of ecological processes, and although IBT is perhaps a useful model for the earliest stages of community assembly on islands it fails to explain the exceptionally high levels of endemism that are often observed [21,46]. To do so requires the evolutionary mechanism of *in situ* speciation, whereby species within the nascent community begin to adapt and diversify, as exemplified by numerous cases of adaptive radiation on islands [47].

The utility of the species pool concept is also strongly impacted by human activity. Humans are rapidly mixing the world's biota and changing the global environment. Consequently, we can view the global introduction of exotic species as an enormous (but uncontrolled) experiment in community assembly. Consider the extent of species introductions in the state of Michigan, USA alone, where there are >100 non-indigenous freshwater species (<http://nas.er.usgs.gov>) and >900 exotic plant species [48]. These species introductions have seemingly occurred with few extinctions of native species (although certainly with large changes in relative species abundances). Applying the species pool definition ('all species available to colonize a focal site' [44]) at the scale of Michigan is challenging because we cannot know the source, or the impact, of the next invasive species.

By contrast, recent studies have shown the potential to test predictions of ecological theory (e.g., species-area and species-isolation relationships) based on knowledge of economic trade routes and the potential for human-assisted species spread [27] as well as testing the relative resistance of tropical and temperate communities to invasion [49]. Thus, as noted by Helmus *et al.* [27] and others, the Anthropocene may provide opportunities as well as challenges for understanding the dynamic nature of species pools and their role in community assembly. At more local scales, the species pool concept has been increasingly applied to problems of restoration ecology and to the management of communities of conservation concern (e.g., [50]). A key issue in these systems involves identifying the pool of species that might be expected to colonize a site, and particularly the composition and abundance of exotic species in the propagule pool.

Concluding remarks: species pools and community assembly – challenging the paradigm

At present, there is a clear divide between biologists interested in evolutionary processes that contribute to the origin and geographical scale of dynamic species pools and those focused on the assembly of local communities

from static species pools. This difference in perspective is clearly illustrated by the lack of ecological and evolutionary feedback from communities to the species pool in the conventional model of community assembly (Figure 1A). Without a better connection to the ecological and evolutionary processes that generate diversity, the notion of the regional species pool stands as an abstract and isolated concept in community ecology. We believe that ecology needs to advance the study of community assembly beyond a deliberation over the relative roles of environmental filtering and species sorting and incorporate evolutionary thinking beyond the consideration of phylogenetic relationships of component species.

To this end, local adaptation, the geography of speciation, and the causes and consequences of secondary sympatry are key issues that require further attention in understanding the dynamics of community assembly. New models for understanding the assembly of regional species pools must resolve the dilemma of how species that evolved in allopatry achieve secondary sympatry (e.g., [41]). For example, if strong local adaptation limits opportunities for secondary sympatry, major environmental perturbations may be required to facilitate range expansion, establishment, and coexistence (Box 2). In this scenario, coexistence of sister species is enhanced when changes to their habitats reduce the degree of local adaptation; in essence, leveling the playing field. We suggest that progress toward understanding community assembly will require new approaches enumerating both the ecological and the evolutionary barriers that may limit the origin, colonization, and coexistence of species in complex landscapes.

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