Trends in Ecology & Evolution

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Opinion

The Ecology of Nonecological Speciation and Nonadaptive Radiations

Jesse E. Czekanski-Moir [1,*] and Rebecca J. Rundell[1]

Growing evidence for lineage diversification that occurs without strong ecological divergence (i.e., nonadaptive radiation) challenges assumptions about the buildup and maintenance of species in evolutionary radiations, particularly when ecologically similar and thus potentially competing species co-occur. Understanding nonadaptive radiations involves identifying conditions conducive to both the nonecological generation of species and the maintenance of co-occurring ecologically similar species. To borrow MacArthur's [1] (*Challenging Biological Problems* 1972;253–259) form of inquiry, the ecology of nonadaptive radiations can be understood as follows: for species of type A, in environments of type B, nonadaptive radiations may emerge. We review purported cases of nonadaptive radiation and suggest properties of organisms, resources, and landscapes that might be conducive to their origin and maintenance. These properties include poor dispersal ability and the ephemerality and patchiness of resources.

Highlights

Nonadaptive radiations result from nonecological speciation and the absence of character displacement.

There are properties of organisms and ecosystems that make nonadaptive radiations more or less likely.

As our understanding of cryptic species increases, we are likely to become aware of more nonadaptive radiations.

Nonadaptive radiations can give rise to functional redundancy in ecosystems, which is likely to be correlated with resilience and/or resistance to perturbation.

Understanding the ecology of why competitive exclusion is mitigated is essential for the conservation of biodiversity.

On the Origin of Nonadaptive Radiations

Thirteen years after the publication of *On the Origin of Species by Means of Natural Selection*, Gulick [2] suggested that the most species-rich groups of land snails in Hawaii might have diversified for reasons having little to do with **natural selection** (see Glossary). Although these species were distinguishable by shell characters, their shells seemed unlikely to be correlated with adaptations to different environments: 'The conditions under which they live are so completely similar, that it does not appear what ground there can be for difference in the characters best fitting the possessors for survival in the different valleys in which they are found'. Gulick thus provided insight into the potential role for nonadaptive pattern and process in evolution [3,4] (as reviewed in [5]) and an unintentional counterpoint for **adaptive radiation**: **nonadaptive radiation**. Nonadaptive radiation entails lineage **diversification** with minimal ecological divergence (Box 1), often (but not always) resulting in allopatric or parapatric taxa [6,7]. It generally involves the proliferation of species that can occur as the result of restriction of gene flow (e.g., as occurs during the formation of a geographic barrier), but the underlying process of species formation is affected by similarity of environments experienced by populations on either side of the barrier. Speciation in nonadaptive radiations therefore does not involve ecologically based divergent selection but instead may occur slowly, through the fixation of different and selectively favored mutations among allopatric populations (Box 2; see Figure 1D). Several recent studies have presented evidence consistent with the idea that species diversity can be generated without concomitant ecological divergence [8–14] (Table 1). Although we still lack a unified conceptual approach to predict what situations give rise to nonadaptive radiations, the increasing number of reports of nonadaptive radiation provide an opportunity to explore the extent to which the mode of evolutionary radiation can be predicted. For example, evidence for nonadaptive radiations often involves organisms with limited dispersal abilities, such as land snails [2,6,7] or certain plants [15,16], perhaps implying that particular species or environments (e.g., highly subdivided

[1]Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210, USA

*Correspondence: jeczekan@syr.edu (J.E. Czekanski-Moir).

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Box 1. Are Nonadaptive Radiations Real?

Coexistence and adaptive explanations for traits should not be treated as *a priori* facts but as hypotheses to be tested [58,108]. It follows that not every clade arises as a result of divergent natural selection. As we mention in the Glossary, 'minimal' differences between organisms and their habitats are inevitable given the large number of measurable variables inherent in each. Warren *et al*. [24] remind readers that there will almost always be measurable differences between two habitats, but that need not imply that those differences (rather than, e.g., barriers to dispersal) have driven their inhabitants on separate evolutionary trajectories. It is also inevitable that differences between species will accumulate due to neutral processes. Because of the 'transient' property of multidimensional random walks [109], the extent of divergence between populations may depend as much on how many traits are measured as on how many generations have elapsed [110,111]. Our understanding of how much morphological divergence can realistically be expected to accumulate among species within a given lineage is still developing, and future simulation studies and analyses of the fossil record are likely to play an important part in our ability to infer process from pattern in evolutionary data [112].

Although we argue that some suspected nonadaptive radiations are not just adaptive radiations waiting to be discovered, as with any scientific endeavor there will be instances where researchers may disagree on the interpretation of data and definitions. For example, what has been called a 'nonadaptive radiation' by Hardy *et al*. in their study of scale insect diet evolution [113] satisfies the definition of an 'adaptive radiation' in this Opinion article and others [7,15,19,114]. The definitional difference is linguistically subtle, but biologically profound. Hardy *et al*. [113] hold that although the number of dietary roles occupied by a lineage increases through time, the process is a 'nonadaptive radiation' because the evolution of dietary specialization in insects that are essentially aeolian plankton is maladaptive. For the purposes of this article, we would still categorize this as an adaptive radiation, because divergent natural selection drives an increase in ecological (especially dietary) disparity through time.

Epistemological issues can also encroach on our ability to categorize evolutionary radiations. In a recent study by López-Estrada *et al*. [115], the authors argue that an extremely morphologically diverse (but relatively taxonomically depauperate) clade of beetles is a nonadaptive radiation because they infer high rates of extinction from a molecular phylogeny of the clade, and they argue that high rates of extinction are consistent with nonadaptive radiations. We urge caution in this interpretation because not only may extinction rates be problematic to infer from molecular phylogenies in the absence of fossils [116,117], but the morphological disparity of the clade in question (especially compared with other, similarly aged beetle clades) suggests that divergent selection has played a nontrivial role in the evolution of this group.

environments with similar habitats and conditions on either side of barriers, such as can occur in mountainous tropical rainforests of oceanic archipelagos or among groups of temperate ponds) might be prone to this evolutionary pattern and the ecological processes that underlie it (Table 2). Here, we explore ecological conditions that are conducive to speciation in the absence of divergent natural selection.

Nonadaptive radiations are of interest because increasing evidence suggests that they might not be uncommon in nature (Table 1). This may be particularly true for old adaptive radiations where reproductive isolation might have evolved slowly over time among similar environments separated by barriers or unsuitable habitat, with species only later subject to ecologically relevant divergence characteristic of adaptive radiations, causing species' morphologies (or physiologies, behaviors, etc.) to diverge and adapt to those new ecological differences [7]. We consider both adaptive and nonadaptive radiations in turn but note that some radiations also contain elements of each, such as *Tetragnatha* spiders [17,18].

The hallmark of adaptive radiations is a link between disparity (e.g., morphological, physiological) and environment (although whether the disparate traits are adaptive can be more difficult to establish [19]). **Disparification** is also central to Givnish's macroevolutionary conception of adaptive radiation, but he suggests that diversification rate should be separately considered [20]. Simpson [21] and Schluter [19], by contrast, incorporate rapid speciation into their concepts of adaptive radiation. Both diversification rate and degree of phenotypic divergence are captured by Jablonski's 'type 1 diversification', where rates or magnitudes of phenotypic divergence are unexpectedly high at some phase in a clade's history [22], which one could

Glossary

Adaptive radiation: (i) a pattern of species diversification in which a lineage of species occupies a diversity of ecological roles [90]; and (ii) the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage [7,15,19].
Beta diversity: can be thought of as the difference between assemblages; in the context of patchy habitats it is sometimes formally defined as the ratio of gamma (regional, or landscape level) diversity to average alpha (local, or patch level) diversity. If a set, small number of species can occupy small habitat patches, increasing beta diversity among patches will necessarily increase gamma diversity.
Coexistence: Siepielski and McPeek [58] make the distinction between co-occurrence and coexistence of species, the latter of which implies some level of population stability among community members at the local scale that is stabilized by species traits and niches. This is in contrast to co-occurrence, where species' presence in a community is largely due to chance or larger-scale processes.
Community assembly: the construction and maintenance of local communities through sequential, repeated immigration of species from the regional species pool. Vellend [68] usefully suggests that species membership in assemblages at various scales is driven by the processes of speciation, extirpation, migration, and ecological drift.
Co-occurrence: refers to species that are found together by chance or because of larger-scale processes, like source–sink dynamics. Neutral species co-occur.
Disparification: increase in the morphospace occupied by members of a clade through time [102,103]; distinct from diversification, which we use here to mean an increase in the number of species in a clade through time. Nonadaptive radiations are expected to exhibit diversification with minimal disparification.
Diversification: net increase in the number of species in a clade over time. Speciation minus extinction.
Ecological drift: random fluctuation in species abundances in an

Box 2. Nonecological Speciation

'It is useful to consider ecological speciation as its own form of species formation because it focuses on an explicit mechanism of speciation: namely divergent natural selection. There are numerous ways other than via divergent natural selection in which populations might become genetically differentiated and reproductively isolated' ([46], see p. 8).

Consistently with Nosil [46] and others [7], we define nonecological speciation as speciation that does not arise from divergent natural selection (see Figure 1D in main text). As discussed previously, it is likely that this usually occurs in allopatry or parapatry, and it might be an important step in some adaptive radiations (particularly old ones) as well as nonadaptive radiations [7]. There are a number of potential mechanisms for nonecological speciation. For example, the order in which new mutations arise and subsequently fix (or are lost accidentally) in geographically isolated populations is potentially important and has been termed mutation-order speciation [118]. More generally, the occasional production of mutations that are favored on a particular genetic background may occur (e.g., those involved in producing an ornament that is subject to sexual selection). The production of such mutations is more likely in large populations [34], which are common in some invertebrates (e.g., land snails). Through accumulation of such mutations, populations on separate evolutionary trajectories eventually evolve reproductive isolation (e.g., due to compensatory substitutions in response to initial internal adaptation of the organism [119]) and thus might speciate nonecologically, particularly when they exist in geographic isolation.

It is likely that, for animals (and perhaps other groups of organisms), speciation in sympatry is more rare [120]. However, there are several convincing examples of ecological speciation in sympatry [46], and nonecological speciation in sympatry may also be possible if the results of mutations are extreme. Polyploid species in plants are likely to evolve in sympatry with one or both of their parent species. Although there is important ecological work in showing instances where ploidy level can provide adaptive advantages [121], the sheer number of variations of polyploidy present in some plant taxa calls into question the idea that there is a selective advantage to every change in chromosome number. Analogously, the appearance of opposite-chirality shells in land snails that restrict mating with the parental population results from a mutation that may or may not be maintained by natural selection [120,122].

Nonecological speciation by genetic drift is unlikely and is not considered here [119]. However drift can exert influence on populations, before, during, and after speciation [123].

ascribe to adaptive radiation. Adaptive radiations tend to occur, or are at least conducive to study, in places that are permissive of allopatric speciation (e.g., due in part to relatively rapid isolation by vicariance or dispersal) and ecological differences (e.g., exposure to novel environments, empty **niche** space due to unbalanced biotas). Both conditions are common among young oceanic archipelagos, which hold some of our premier examples of adaptive radiations [17,19,23]. Adaptive radiation might also occur in sympatry in certain cases under particularly strong divergent selection. Species in adaptive radiations form sympatrically when barriers to gene flow evolve due to ecologically based divergent selection (**ecological speciation**), which can be rapid. This is encouraged and accelerated by character displacement (e.g., evolutionary change in bill depth and width in seed-eating bird species competing for resources) or ecological opportunity. As discussed in Rundell and Price [7], routes to adaptive radiation fall on a continuum involving, at one end, the coupling of ecological differentiation and the evolution of reproductive isolation, or, at the other end, the slow achievement of reproductive isolation followed much later by ecological differentiation.

In contrast to adaptive radiation, nonadaptive radiation is lineage diversification with minimal ecological differentiation, with the caveat that there are likely to be slight differences among species since all environments differ slightly [24]. Similar to adaptive radiations, nonadaptive radiations might be achieved by various routes, which makes absolute generalizations about their tempo and geography difficult. Classic examples are typified by geographically nonoverlapping (allopatric) species [7]. In nonadaptive radiations that are driven by allopatric speciation, we predict that the buildup of species would proceed slowly. If barriers previously restricting gene flow (e.g., disruptive landforms in combination with low dispersal) were to dissolve, incipient species in nonadaptive radiations might also collapse or go extinct (Figure 2B,C).

assemblage, analogous to genetic drift of allele frequency in a population (see [68]).
Ecological speciation: the generation of reproductive isolation between populations as a result of ecologically based divergent selection between environments, which can include both natural and sexual selection [34,46].
Janzen–Connell–Thingstad dynamics: a family of **negative density-dependent selection (NDDS)** or negative frequency-dependent selection (NFDS) processes that are very similar, although Janzen–Connell is typically invoked by tropical forest biologists, whereas Thingstad's 'Kill-the-Winner' hypothesis is much more frequently cited in the marine phage literature [86,87].
Natural selection: differential survival and/or reproduction of classes of entities (alleles, genotypes, subsets of genotypes, populations, species) that differ in one or more characteristics.
Negative density-dependent selection (NDDS): sometimes referred to as 'inverse' density-dependent selection; selection that favors rare phenotypes. Although technically distinct, NFDS has similar effects on community-level dynamics, as frequency is often related to density. One way that NDDS and NFDS dynamics can arise is through species-specific pathogens, which will tend to lead to some variation of Janzen–Connell–Thingstad dynamics. Another possible way that NDDS or NFDS can occur is through sexual conflict [61,104]. Throughout this Opinion article, we refer to population dynamics among (not within) species; that is, our discussion focuses on species richness rather than intraspecific genetic diversity.
Neutral species: species that are ecologically nearly identical to one another and that follow the neutral dynamics of a random walk in relative frequency as described by Hubbell [105]; one of the four types of species in a community identified by McPeek [69] based on their population dynamical properties.
Niche: the environmental conditions that allow a species to satisfy its minimum requirements so that the

Other modes of speciation, like polyploidization, can lead to reproductive isolation in a generation. In these cases nonadaptive radiation will involve rapid diversification. Because both adaptive and nonadaptive radiations are multifaceted phenomena, other authors have argued for the creation of more finely partitioned categories [25] or elimination of the term 'radiation' altogether [26]. Although precise delimitation can be difficult, we suggest that the terms adaptive and nonadaptive radiation should be retained as ways of discussing the drivers of diversification.

To understand nonadaptive radiations, we must understand both how net diversity can increase via **nonecological speciation** and why species do not always drive each other extinct if there is range overlap. Below, we review mechanisms that generate diversity and provide an ecological framework to identify nonadaptive radiations and understand how they might arise and persist. This follows from observations about the biology of species frequently implicated in nonadaptive radiations and the properties of organisms and resources that potentially promote nonadaptive radiation (Table 2). Next we discuss geographical distribution as it pertains to nonadaptive radiation. We then explore ecological conditions that mitigate competition among ecologically similar species in similar environments (e.g., those focused on the same resource) and might therefore be permissive of nonadaptive radiation. We show that nonadaptive radiations are genuine phenomena that illustrate important aspects of ecology and evolutionary biology.

Properties of Organisms

Since nonadaptive radiations involve both elevated diversification and lack of clade-wide disparity in resource usage, identifying the properties of organisms connected with these factors should help us both uncover and understand nonadaptive radiations. Diversification and lack of disparity may often have different mechanistic underpinnings, so it is useful to consider them separately (Table 2). Understanding which species are prone to geographic isolation and thus allopatric speciation is of interest since our clearest cases of nonadaptive radiation occur in allopatry [7]. Organisms that are poor dispersers should be more prone to allopatric speciation, even within relatively small geographic areas [27–29]; at larger spatial scales, organisms with intermediate dispersal abilities might have the highest diversification rates, since they are good enough at dispersing to colonize new areas but not good enough to maintain gene flow after a jump dispersal event [30]. The possibility of subsequent range overlap is part of the reason dispersal ability can be complicated: if there is a continuous rain of propagules arriving from the parent population, speciation may never occur, so taxa with large dispersal abilities may speciate more slowly. However, occasional rare dispersal events are very important on geologic timescales for some modes of allopatric speciation (especially in the islands of the remote Pacific [31]). Therefore, those organisms that are the poorest dispersers (e.g., Cyphophthalmi opilionids, which seem to exhibit almost perfect vicariance [32,33]) can be locally diverse in their ancestral ranges but may never reach new islands where they might diversify.

Note that poor dispersal ability might affect not only the early colonization stage of speciation but also the ability of populations to become established in new locations [34]. Presumably this could slow speciation rates in nonadaptive radiations. A variety of organismal traits are correlated with dispersal ability, including the ability to fly (or have propagules dispersed by a flying organism [35,36]), the presence of a planktonic larval stage [37], and wind-dispersed seeds, pollen, or spores [16,38]. Adult body size is positively correlated with dispersal ability in many animals, but this relationship seems to have an inflection point around 2 mm, since microscopic organisms often have large geographic ranges (although sometimes not as large as morphological species concepts might suggest) [39,40].

birth rate of a local population is equal to or greater than its death rate, along with the set of *per capita* effects of that species on these environmental conditions [70,106].

Niche conservatism: a pattern where closely related species are more ecologically similar to one another than would be expected based on their phylogenetic relationships. Niche conservatism is not expected in an adaptive radiation.

Nonadaptive radiation: lineage diversification with minimal ecological diversification, often (but not always) resulting in allopatric or parapatric taxa. 'Minimal' refers to slight differences among species that can accumulate in allopatry; for example, due to neutral evolution or slight differences in environments [24] (Box 1).

Nonecological speciation: the generation of reproductive isolation between populations that does not arise from divergent natural selection [46]. One potential mechanism by which nonecological speciation can occur involves the slow process of fixation of different and selectively favored mutations among allopatric populations.

Priority effects: a pattern whereby the outcome of competition for a resource is highly influenced by the (often stochastic) order of arrival. For example, some types of wood-rot fungi will be able to exclude competitors only if they are established first [70,80]. A related mathematical model of stochastic community assembly is the 'Lottery Hypothesis' [78,107].

Probability refuge: a metaphorical 'refuge' concept that Shorrocks and others [60,71,72,75] invoke in the aggregation model to describe the niche space that opens for ecologically similar species when intraspecific competition is stronger than interspecific competition (e.g., due to aggregated egg laying and sibling competition in ephemeral patchy resources).

Sexual selection: selection on traits resulting from differential mating success, including access to different numbers of mates or to mates of differing quality [34] (Box 3).

Sink species: species that are present only due to continual

The properties of organisms that make them more or less likely to exhibit clade-wide disparity with respect to resource use are more recalcitrant to study than the organismal correlates of diversification. Macroevolutionary patterns like **niche conservatism** or radical departures thereof (Jablonski's [22] type 3 and type 1 diversifications, respectively) are difficult to study directly. An observation of strong niche conservatism in a clade is consistent with a nonadaptive radiation, but the extent to which niche conservatism arises from properties of the organism (endogenous) versus the stabilizing selection that arises from the organism in its environment (exogenous) is unclear and is likely to be different for different taxa [41,42]. Similarly, the mechanistic underpinnings of morphological and niche disparity (or lack thereof) are incompletely understood. Some researchers have suggested that phenotypic differentiation through plasticity might be an important early phase of character displacement, which then leads to the evolution of genetically based morphological differences among some species in certain environments [43,44]. If this is true one could speculate that perhaps species that are less prone to phenotypic plasticity would be less likely to diversify via character displacement. Differential gene expression might also be relevant to understanding species susceptibility to niche differentiation and disparification, since in some cases it might underlie species persistence in new environments, and even the adaptive genetic divergence driving ecological speciation [45,46].

Organisms' genomes might also influence diversification or disparification. With respect to nonadaptive radiation, polyploidy is a nonecological mechanism that can lead to speciation in sympatry, particularly in plants [46] (Figure 3D). There is also growing evidence that large-scale genome duplications coincide with diversification and sometimes ecologically relevant morphological differentiation on macroevolutionary timescales (e.g., in hexapods and angiosperms [47,48]).

Finally, certain organisms and traits seem to be particularly prone to **sexual selection**, which can lead to nonadaptive radiation. Mate signaling and other mechanisms of prezygotic isolation are uncontroversially tied to diversification; for example, song divergence in *Laupala* crickets from the Hawaiian Islands [49], electric signals in Gabon riverine fishes (family Mormyridae) [50], and speciation by song-learning in passerine birds [51]. In some cases, species differences might have evolved first and rapidly via sexual selection (e.g., electric organ discharge in mormyrids [50]), with morphological adaptations perhaps accumulating later via natural selection [50]. We discuss the potential for diversification in nonadaptive radiation via sexual selection in Box 3.

Geography of Nonadaptive Radiation

Geographic distribution is important for understanding species' evolution and ecology but its interpretation with respect to diversification mode is not always straightforward. Many presently sympatric species are likely to have speciated in allopatry at some point prior. The underlying process at the time of speciation, millions of years ago in some cases, can be difficult to uncover [52], which complicates our understanding of both adaptive and nonadaptive radiations. Many currently sympatric species are quite old and may have diverged nonecologically [34]. In young adaptive radiations such **co-occurrence** is less difficult to understand due to the potential for competitive exclusion. However, it is difficult to rule out the potential for speciation to have occurred initially in allopatry and by nonecological means, with ecological differences evolving later [7]. Species' ability to co-occur suggests ecological differences in many, if not most, cases. For this reason we would expect most nonadaptive radiations to be composed of species that are allopatric or parapatric replacements of one another, as is the case for nonadaptive radiations of some Hawaiian land snails (Achatinellidae, Amastridae) and California salamanders (Plethodontidae) [2,7,53]. However, some nonadaptively radiating species co-occur, such as *Blepharoneura*

migration from other communities; one of the four types of species in a community identified by McPeek [69] based on its population dynamical properties.

Source–sink dynamics: movement of individuals between high-quality (source) and lower-quality (sink) patches within a metacommunity, where populations in the sink are sustained only through migration.

Walking-dead species: species that are slowly being driven extinct by the ecological conditions that they experience within the community – immigration will not rescue them; one of the four types of species in a community identified by McPeek [69] based on its population dynamical properties.

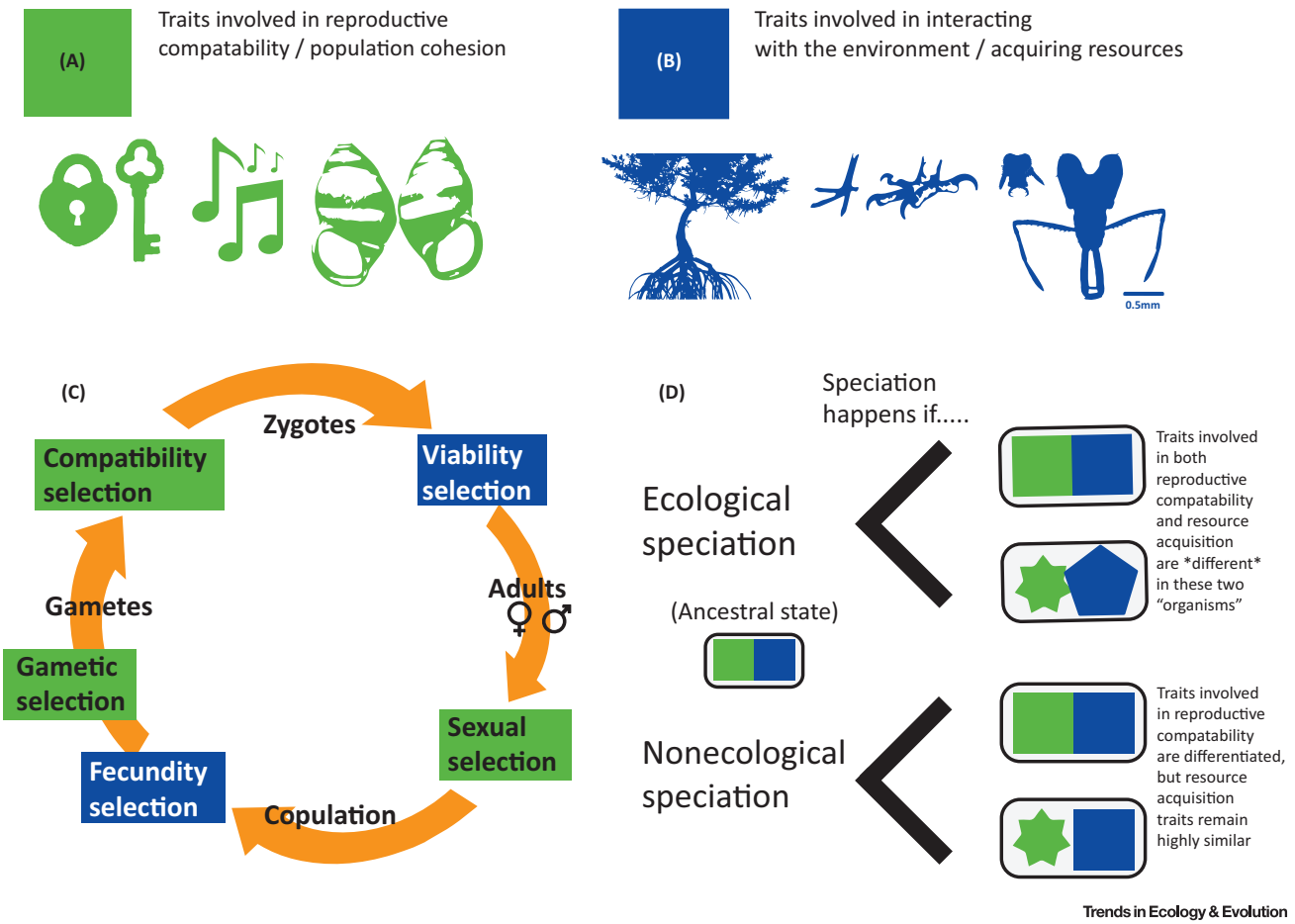


Figure 1. A Two-Way Classification of Organismal Traits (A,B, Top Panel) As They Pertain to Nonecological and Ecological Speciation. Organismal traits that are involved in nonecological speciation might include morphological or behavioral correlates of prezygotic isolation, such as 'lock-and-key' mechanisms, bird song, or snail shell chirality (A). Traits involved directly in ecological speciation might include adaptations to different environments or different methods of acquiring resources (e.g., ant mandibles, bird feet (B)). Note that, in some cases, there is a direct link between the 'blue' and 'green' traits (e.g., flower traits involved in attracting pollinators). The potential involvement of different classes of traits as they pertain to the components of fitness during a hypothetical organismal life cycle is shown in (C). Components of fitness that involve reproductive compatibility traits are indicated in green and components of fitness involving resource acquisition traits are shown in blue. The expected patterns of ecological versus nonecological speciation are shown in (D). Note that, in ecological speciation, traits involved in reproductive compatibility or population cohesion (green shapes), as well as those involved in resource acquisition (blue shapes), differentiate. By contrast, nonecological speciation is characterized by lack of differentiation in traits involved with resource acquisition (indicated by blue squares). Images in the upper right are ant heads modified from specimen photographs from antweb.org (CASENT0133445 photographed by Erin Prado; CASENT0178461 photographed by Michele Esposito).

tropical fruit flies, where lineages originated allopatrically and subsequently built up non-interbreeding populations within communities without shifts in host use [54], and *Naja* aquatic plants, which seem ecologically identical but differ in ploidy and may represent an example of sympatric nonecological speciation [55]. Some congeneric, reproductively isolated odonate insects also possess overlapping niches and geographic ranges [9,56,57]. For example, diversification in *Enallagma* damselfly species has occurred without obvious ecological divergence [57,58] and in some cases reproductive isolation, not completed in allopatry, is in progress (i.e., tactile and mechanical aspects of mating structures) among these young species where their geographic ranges overlap [56]. Models also suggest that co-occurrence among functionally similar species might be possible [59–61].

Table 1. Exemplar Organisms and Types of Evidence in Nonadaptive Radiations and their Associated Key References

Type of evidence/organism or ecological pattern in simulation or theoretical study	Refs
Anecdotal evidence consistent with nonadaptive radiation	
Achatinellidae, Amastridae, *Albinaria* (Clausiliidae) land snails	[2,6]
Ecological evidence consistent with nonadaptive radiation (ecological interchangeability)	
Cryptostigmata oribatid mites	[77]
Ascomycota and Basidiomycota wood-decaying fungi, Saccharomycetales nectar yeasts, arbuscular mycorrhizal fungi	[80,81,88]
Calopteryx (Calopterygidae), *Enallagma*, *Ischnura* (Coenagrionidae), Calopterygidae damselflies, and *Drosophila* (Drosophilidae) fruit flies	[9,57,75,127,132]
Evolutionary evidence consistent with nonadaptive radiation (e.g., increase in disparity decoupled from increase in species richness)	
Thraupidae, Furnariidae passerine birds	[51]
Mormyridae riverine fishes	[50]
Blepharoneura (Tephritidae) flies	[54]
Phymaturus, *Liolaemus* (Liolaemidae), *Eutropis* (Scincidae) lizards	[11,14]
Cricetidae and Sigmodontinae (sigmodontine rodents)	[8]
Ambystoma macrodactylum long-toed salamander species complex, *Batrachoseps* (Plethodontidae) salamanders	[10,53]
Simulation/theoretical studies consistent with nonadaptive radiations	
Janzen–Connell–Thingstad dynamics	[86,89,96]
Aggregation model	[60]
Sexual conflict leads to negative density dependence	[61,104]
Cryptic species that seem unlikely to have strong ecological differentiation	
Najas (Hydrocharitaceae) aquatic flowering plants	[55]

When lineages diversify nonecologically in allopatry (a common case of nonadaptive radiation), populations might later come back into contact with each other. At that point a number of outcomes are possible: extinction via introgression [62,63], extinction via competitive exclusion [63,64], character displacement [65,66], or none of these things (Figures 2 and 3). If range overlap cannot occur because of competitive exclusion or incomplete reproductive isolation, diversification should slow (Box 4). In the next section, we describe some of the ecology of why both competitive exclusion and character displacement might be avoided (as in Figures 2 E and 3 B,D).

Community Ecology of Avoiding Competitive Exclusion

In this Opinion article, we treat competition for resources as the primary factor that usually prevents geographic range overlap between ecologically similar taxa. Competitive exclusion is most convincingly demonstrated in small areas (e.g., Petri dishes [64]), but many taxa exist in metapopulations where local extirpation can be balanced by dispersal [67,68]. Patchily distributed, ephemeral resources are permissive of a variety of processes that can allow high degrees of niche overlap at regional scales. These processes include **source–sink dynamics** and **ecological drift** [67–69]. Below, we review two patterns of community ecology that might permit the co-occurrence of ecologically equivalent species: those where intraspecific aggregation [60] or **priority effects** [70] dominate.

Table 2. Properties of Organisms and Their Milieux That Promote Propensities for (A) Speciation, (B) Clade-Level Disparity, and (C) Mitigation of Competitive Exclusion[a]

Hierarchical level	(A) Propensity to speciate	(B) Propensity for clade-level disparity	(C) Mitigation of competitive exclusion
Genome	Tolerance of polyploidization	Developmental robustness	
Organismal	Asexuality Poor dispersal ability 'Direct development' of marine invertebrates Selfing Structural constraints (evo-devo of niche conservatism?)	Reliance on mutualism for reproduction (e.g., animal pollinator) Mating occurs in or on food source (e.g., *Rhagoletis*)	r-selected propagules that always lose competitions to later ontogenetic stages (e.g., corals, some trees, multicellular fungi); aggregated oviposition, especially holometabolous insects (aggregation model)
Resources (bottom-up limitations)	Patchy, ephemeral; endoparasitic on hosts	Bottom-up limited system, requiring coexistence via tradeoff, or niche shift	Patchy, ephemeral (priority effects, aggregation model) Intermediate or frequent disturbance
Enemies (top-down limitations)	Fewer enemies (release from predation pressure in island adaptive radiations)	Not strongly top-down limited, especially by species-specific enemies	Moderately to strongly top-down limited by species-specific enemies (Janzen–Connell–Thingstad)
Landscape/climate	Many geographic barriers (e.g., an archipelago, mountain 'sky islands')	Adjacent, disparate climates/soil types	Proximity to other very similar habitat patches (source–sink dynamics)

[a]If properties in columns (A) and (B) are exhibited, an adaptive radiation might emerge. If a clade exhibits properties listed in columns (A) and (C), a nonadaptive radiation is more likely. Note that individual taxa are unlikely to exhibit every property in a given column. Some nonadaptive radiations might have properties listed in column (B); for example, Winkler *et al*.'s [54] *Blepharoneura* (Insecta: Diptera: Tephritidae) system has host specificity similar to *Rhagoletis* (column B), but also undergoes top-down limitation from parasitoids (column (C)).

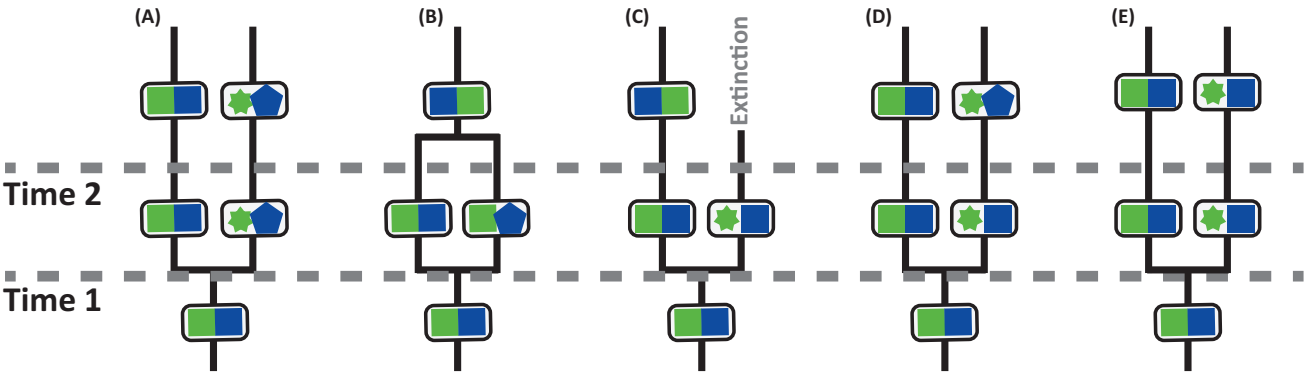
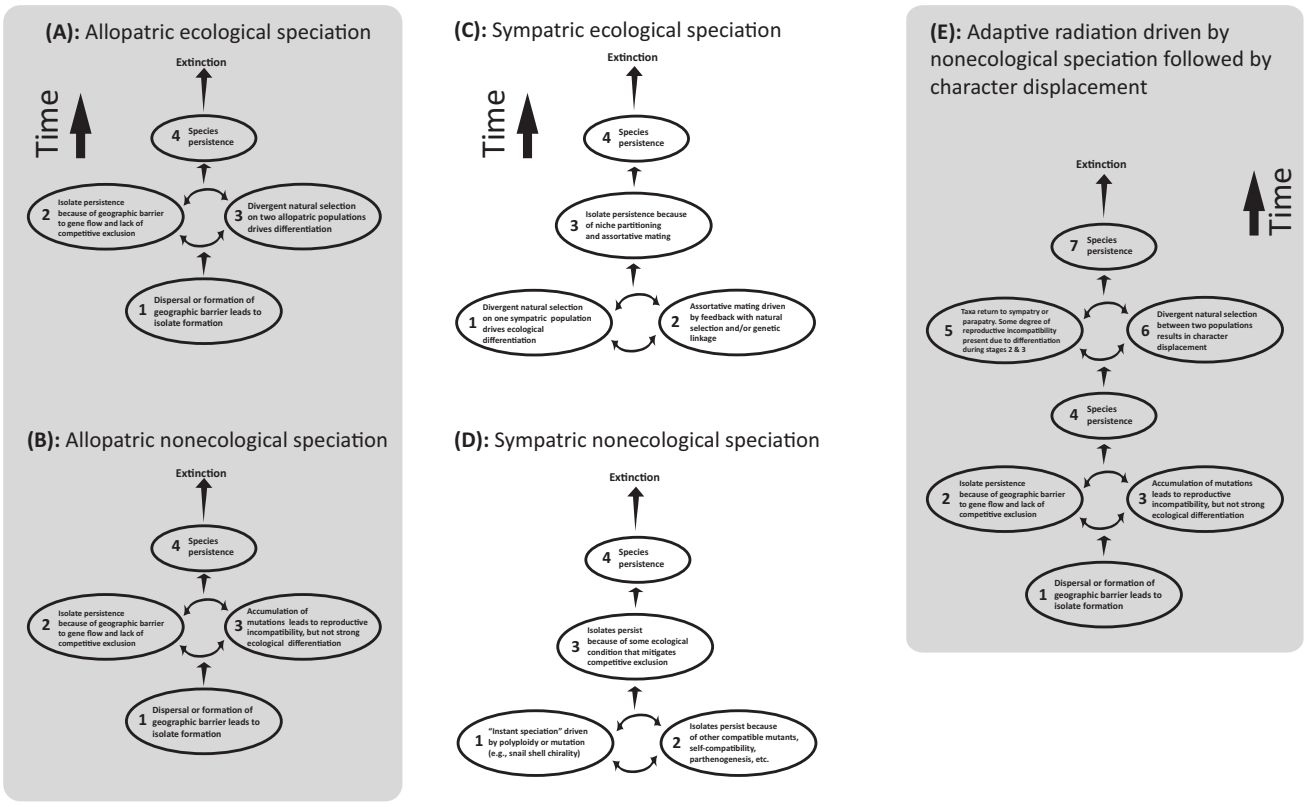


Figure 2. Different Possibilities of How Lineages Could Diverge in Allopatry (Time 1) and Then What Might Happen When the Barrier is Removed and the Species or Incipient Species Come Back into Contact (Time 2), with Reference to Traits Involved in Reproductive Compatibility (Green) and Traits Involved in Interaction with the Environment or Acquiring Resources (Blue; Figure 1). In the different speciation events: (A) Represents ecological speciation in allopatry, followed by a return to sympatry with the two taxa persisting because there are trait-based mechanisms for both niche partitioning and assortative mating (differences in the blue and green shapes, respectively). (B) Represents the beginning of ecological differentiation in allopatry, then extinction by introgression (collapse of incipient species) when the populations come into contact again (this is a conservation biology concern with, e.g., the spread of some fish subspecies between watersheds; no difference in the green shapes). (C) Nonecological speciation in allopatry, followed by extinction by competitive exclusion when there is a return to sympatry (different green shapes but same blue shapes). (D) Nonecological speciation in allopatry, followed by character displacement when there is a return to sympatry (green shapes differentiate after time 1, blue shapes differentiate after time 2). (E) Nonecological speciation in allopatry, followed by lack of either extinction or character displacement when there is a return to sympatry (green shapes differentiate after time 1, blue shapes never strongly differentiate). The ecological plausibility of case (E) after time 2 is a primary theme of this Opinion article. Note that both case (D) and case (E) are nonecological speciation, whereas only (A) is ecological speciation in the strictest sense; however, case (A) and case (D) might be empirically impossible to differentiate in many cases. There are other combinations of processes possible (e.g., 'reproductive character displacement'; [56,66] and Box 3).



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Figure 3. An Elaboration of Allmon and Sampson's [131] 'Stages of Speciation Framework', Which We Have Modified to Illustrate How Some of the Different Types of Speciation and Radiation Unfold. The time axis indicates the direction of the sequence of stages and is not to scale. Note that time proceeds from the bottom to the top of the figure (as it does in the stratigraphic record). The paleobiological perspective that Allmon and Sampson bring to discussions of speciation remind us that all species will eventually go extinct, which is why 'extinction' is included as a final stage in each case. Cases described by (A,C,E) could all lead to adaptive radiation. (E) is discussed further in [7,66]. (B,D) would lead to nonadaptive radiations. (A) (Ecological speciation in allopatry) is equivalent to Figure 2A. When species become sympatric they persist due to the evolution of trait differences involving both reproduction and resource acquisition. The conditions in the main text under the heading 'Community Ecology of Avoiding Competitive Exclusion' and Table 2 column (C) are relevant at stage 3 in (D) (nonecological speciation in sympatry); that is, we elaborate on what is meant by 'some ecological condition that mitigates competitive exclusion'. (E) is equivalent to Figure 2D (nonecological speciation in allopatry, followed by character displacement when the populations come back into contact).

Aggregation Model

The aggregation model of **coexistence** was developed to describe how intraspecific larval competition could promote the coexistence of flies specialized to lay eggs on the same spatially disjunct and ephemeral resources [71,72]. In the drosophilids that Shorrocks and colleagues were studying, intraspecific aggregation was produced by both the patchiness of the larval habitats and the oviposition behavior of mother flies. These flies would lay a surplus of eggs in the same rotting substrate, so siblings would grow up competing most strongly with each other (in earlier publications, the niche space opened by intraspecific aggregation was referred to as a '**probability refuge**'). For those species in the guild that would otherwise be competitively dominant, aggregation introduces a population limit imposed by intraspecific competition. For all species involved, intraspecific aggregation and the ensuing intraspecific competition lowers the carrying capacity of a patchy environment below that of the sum of its patches, which allows more species to co-occur than would be possible on a continuous resource [73].

Box 3. Sexual Selection in Nonadaptive Radiation

Sexual selection involves reproductive traits and mating, which makes it an important potential contributor to the evolution of reproductive isolation, or speciation. It is useful to consider sexual selection separately from natural selection and ecological differences since it can operate independently from, and sometimes opposing, them [19,34]. Sexual selection can be included within ecological speciation when it is tied to divergence between ecological environments [46,124]. This would include cases where there is connection between the signal and resource access, differential selection on vocal versus visual cues in dense forests versus open habitats [34], and/or sensory biases in females [69]. However, speciation through sexual selection can also occur nonecologically; for example, through female choice for extreme values of male traits (sexual conflict or runaway sexual selection) [46]. Nonecological speciation through sexual selection includes differentiation among species in allopatry or parapatry [34]. This is particularly interesting for its potential contribution to nonadaptive radiations, since it provides a potential explanation for the co-occurrence of ecologically similar species following range expansion. McPeek notes that sexual selection and mate recognition differentiation can result in new species with small or no ecological differences from their progenitors [69]. This has been shown in the evolution of reproductive isolation in the early stages of speciation in sympatric, ecologically similar species (e.g., the evolution of tactile and mechanical incompatibilities involving male external reproductive structures and female choice [56] and wing patch recognition [125,126] in damselfly species). Species that have diverged through sexual selection may remain ecologically and morphologically similar in every way except their reproductive traits. Where such species expand their ranges to inhabit different communities, each with different co-occurring species, additional divergence in reproductive traits might occur. A special case of this occurs when the direction of this divergence differs depending on which related species are present in that particular assemblage. In this scenario, if a particular population diverges enough, its members might no longer be recognized by mates of its own species dispersing from neighboring populations. This is called reproductive character displacement speciation, which might result among species better able to disperse, such as damselflies. Speciation and extinction rates might also be affected by sexual selection. This has been demonstrated to some degree with respect to sexually selected wing pigmentation in weakly ecologically differentiated damselflies [127], with the caveat that inferring extinction rates from molecular phylogenetic data without fossils can be difficult [116,117].

Probability refuges emerge when species within a guild have a stronger tendency to aggregate – and thus compete – intraspecifically [60,71]. While density-dependent intraspecific competition is possible, and perhaps even required in any niche model of coexistence [73,74], in the aggregation model intraspecific competition of the otherwise competitively dominant species is the main factor that promotes coexistence. Probability refuges underlie the coexistence of a

Box 4. Diversity and Diversification

'The most prolonged radiation, however, finally reaches a time when rates of origination, averaged over the whole, fall off rapidly' ([21], see p. 229).

According to many evolutionary biologists, the hallmark of adaptive radiations is a rapid increase in lineages and morphological disparity followed by a period when net diversification slows substantially (but see [20,25]). This expectation likely has to do with the exploitation of ecological opportunity (e.g., many diverse resources) early in an adaptive radiation. When lineages are plotted through time, the gestalt resembles a graph of a population growing exponentially and then achieving carrying capacity. This later phase in an adaptive radiation is said to exhibit negative diversity-dependent diversification (DDD). Ecologically, a slowdown in diversification rate is expected when all niches that could be exploited by a clade have been filled and competitive exclusion and evolutionary constraint prevent further lineage proliferation. In an influential study, McPeek [128] showed in simulations of adaptive radiations that niche space should eventually saturate, which should slow diversification to zero for a time (until a new ecological opportunity arises), whereas in nonadaptive radiations diversification might be unbounded. Thus, the lack of negative DDD in simulated nonadaptive radiations emerged as a possible way to differentiate adaptive from nonadaptive radiations, using dated phylogenies. However, McPeek's simulations were not spatially explicit, so there may still be a role for negative DDD in nonadaptive radiations as well. In a spatially explicit simulation assuming that speciation was allopatric, Pigot *et al*. [129] demonstrated that DDD could also occur in a purely geographic nonadaptive radiation. Further examples of the dynamics of DDD are reviewed by Moen and Morlon [130]. DDD remains an interesting pattern, but we currently lack a good predictive framework regarding when it is expected. How big is niche space? How permissible is range overlap? It is possible that, for nonadaptive radiations in which geographic range overlap is permissible, DDD might be absent and diversification unbounded. But because we still lack a predictive framework regarding how diverse and disparate a clade should become before diversification slows, both the presence and the absence of DDD remain difficult to interpret without extensive knowledge of the biogeography and community ecology of the clade in question.

species-rich guild of *Drosophila* on Barro Colorado Island [75], several other guilds of drosophilids from temperate and tropical areas [76], and a guild of fungivorous soil mites in a Norwegian forest [77]. The aggregation model seems to have the most promise in application to insects that mate and lay eggs on patchily distributed, ephemeral resources and behave in certain (biologically realistic) ways with respect to dispersal [60]. Investigations of the applicability of this model to other systems would be interesting, but even if the aggregation model applies only to insects this is still a nontrivial proportion of global diversity.

Priority Effects

A priority effect occurs when **community assembly** is contingent on the order in which species arrive at the resource patch or habitat [70] (see discussion of the 'Lottery Hypothesis' in [78] and references therein). On long evolutionary timescales, and in resources that are not highly patchy and ephemeral, priority effects can result in the dominance of one or a few lineages in particular ecosystems [70,79]. However, for organisms that exploit patchy, ephemeral resources and/or habitat patches, priority effects present a way in which species produced in nonadaptive radiations might persist despite overlapping niches [72].

Species diversity in priority effect-driven metacommunities on patchy, ephemeral resources results from the interplay between a highly stochastic process (propagule dispersal) and a deterministic process (whichever species colonizes the patch first becomes competitively dominant on that particular patch). Stochastic arrival order and local-scale competition at patches gives rise to interpatch (**beta**) **diversity**, and elevated regional (gamma) diversity that would be impossible if the resources were all contiguous. Priority effects are one of the ways metacommunities can include species that locally co-occur in the short term (one to a few generations) but do not coexist in the long term as species are added and subtracted neutrally from each patch-level community. McPeek [69] assigns species of this nature the potentially difficult to experimentally disentangle categories of 'neutral', 'sink', and **'walking-dead' species** (see also Leibold and Chase's discussion and critique of the 'four archetypes' of metacommunities in [67]). Membership in these species categories can change for any one species depending on the particular community in which that species finds itself [69]. Note that co-occurring neutral or **sink species** present potential landscape-level mechanisms through which populations might avoid extinction over time and thus facilitate sympatry of ecologically similar species in some cases. Although this seems most likely for **neutral species** (i.e., species that are ecologically nearly identical), in areas where metacommunity dynamics among patches dominate, populations of sink species might allow a species to persist.

Priority effects and other stochastic mechanisms of the maintenance of elevated gamma diversity in a patchy metacommunity might be particularly important for guilds of sessile organisms that have a highly vagile but undirected dispersal phase at some point in their life histories and chemical or other means of monopolizing resources once they settle. A well-documented example is Fukami *et al*.'s study of wood-rot fungi [80]. Peay *et al*.'s work with priority effects in nectar yeasts [81] is potentially analogous to the recent Cotoras *et al*. study on spiders in Hawaii [18]; in both cases, closely related species seem to be more ecologically equivalent than some more distantly related taxa, which may make nectar yeasts a compelling complementary system in which to study the adaptive and nonadaptive phases of diversification. Other taxa that have traits consistent with what we would expect for important priority effects in community assembly include other types of fungi, some sessile marine invertebrates [82,83], and plants with wind-dispersed seeds.

Species-specific Top-down Limitation Kills the Winner

Certain forms of top-down limitation might also mitigate competitive exclusion among species produced in nonadaptive radiations. Populations are top-down limited when organismal abundance is limited primarily by, for example, predators, pathogens, or parasitoids. If the agent of top-down limitation is species specific (or learns to be better at hunting the most common species), this can result in negative (or inverse) density-dependent selection. For example, the diversity of tropical rainforest trees is frequently explained by Janzen–Connell effects, which predict greater top-down pressure where species are more common [84,85]. In marine plankton (especially bacteria), Thingstad [86,87] proposed a related model colorfully dubbed the 'Kill-the-Winner' hypothesis in which species-specific bacteriophages will knock back the abundance of the (temporarily) most abundant bacterial plankton. Thingstad's model is similar to Janzen–Connell dynamics [87], thus we refer to **Janzen–Connell–Thingstad dynamics** as a way of providing a conceptual umbrella for this pathogen-driven family of community dynamics (Table 2). More complicated cases of the long-term persistence of species-rich assemblages with broad niche overlap might be driven by Janzen–Connell–Thingstad effects in conjunction with small-scale positive density dependence driven by mutualisms [88].

Although these models are agnostic with respect to speciation mode, they suggest biologically realistic mechanisms by which competitive exclusion might be mitigated among close relatives with broad niche and geographic range overlap, even in a fairly homogeneous habitat with evenly distributed resources [67,87,89] (Figure 3). Janzen–Connell–Thingstad effects would be more likely to be present in ecosystems where the prey or host clade is not a recent arrival, since range expansion is often (but not always) accompanied by a release from top-down pressure [90]. If we do not consider predators or parasites a 'resource', Janzen–Connell–Thingstad effects are permissive of nonadaptive radiations within one clade, while in some cases presuming an adaptive radiation of the clade exerting top-down pressure (i.e., the parasite or pathogen) on the first clade (the resource).

Concluding Remarks: Macroecology and Conservation Biology of Nonadaptive Radiations

If there is a large-scale geographic gradient of one of the properties of resources and/or habitats that is conducive to nonadaptive radiations, one might expect nonadaptive radiations to be more likely in some places than in others. Chase [91] showed that stochastic assembly is more important in more productive environments (as measured by available phosphorus). This could lead to a positive relationship between species richness and productivity at regional scales that include many smaller subcommunities [91]. For systems in which ephemeral, patchy resources are necessary for the maintenance of an ecologically undifferentiated guild, the time it takes for the resource patches to become uninhabitable might alter the gamma diversity of the system. In hot, dry climates, it is likely that small patchy resources like rotting mushrooms and dung are inhabitable for less time than they are in cool, moist environments, and this would be likely to have an impact on the extent to which priority effects occur. The extent to which different climates and levels of nutrient availability are permissive of priority effects and the aggregation model of coexistence could be an interesting area of future research. Ritchie [92] includes parameters for resource quality, but his theory does not fully integrate with metabolic ecology and ecological stoichiometry theory. The interplay of climate, resource quality, and organismal traits is likely to continue to be a fruitful area of exploration in experimental and theoretical ecology (see Outstanding Questions). Studies about the relative importance of niche and neutral community assembly processes within large-scale gradients (e.g. [93]) remain rare, and future such studies are likely to inform our understanding of the geographic distribution of nonadaptive radiations.

The most obvious macroevolutionary consequence of nonadaptive radiations is the generation of clades of functionally redundant species (see Box 4 for a discussion of the tempo of nonadaptive radiations). Functional redundancy is likely to play an important role in ecosystem stability [94,95]. A variety of guilds are likely to harbor the products of nonadaptive radiations, including flies that oviposit in rotting materials [71,75], land snails [2,6], certain rodents [8], and perhaps certain rainforest trees and scleractinian corals [96]. If one species from one of these guilds goes extinct, it is likely that its role in the ecosystem can be filled by other, closely related organisms [97]. A key to the link between redundancy and resilience in ecosystems is that not all of the 'redundant' species can respond in the exact same way to perturbations [95,98]. It is possible that very closely related species might have similar responses to a new parasite or pathogen, but in many cases species diversity can slow the spread of diseases that might otherwise decimate a guild of stony corals or rainforest trees [99]. This is the same mechanism that underpins Janzen–Connell–Thingstad-type dynamics [84–86].

The conservation biology of nonadaptive radiations will hinge on a better understanding of the ecology of different types of evolutionary radiations than we currently have. In nonadaptive radiations in which all lineages are allopatric, prevention of human transport of species is essential to prevent geographic homogenization of the clade [100] through extinction driven by introgression or competitive exclusion (Figure 2B,C). In radiations in which a resource or landscape property prevents extinction by mitigating competitive exclusion, particular landscape or habitat features might be essential to the survival of lineages. Ultimately, a better understanding of the ecology of nonadaptive radiations includes an understanding of the mechanisms by which extinction rates slow below the rates of speciation. Both community ecology and evolutionary biology would be well served by a more complete and predictive understanding of extinction. And many would argue that such an understanding is an urgent conservation need [101].

Outstanding Questions

What genomic, organismal, and ecological factors determine the limits of clade-level disparity?

What genomic properties predispose lineages to undergo nonecological speciation via polyploidy or other mechanisms of genomic incompatibility?

What levels of clade-level disparity are expected under neutral evolution and how does this scale with the dimensionality of the morphospace being examined?

Does the macroecology of priority effects relate to large-scale diversity gradients?

To what extent do ecologically redundant species generated by nonadaptive radiation lead to ecosystem stability?

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