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# Coexistence in Close Relatives: Beyond Competition and Reproductive Isolation in Sister Taxa

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## Keywords

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## Abstract

Understanding coexistence of closely related species lies at the nexus of disentangling how historical and ecological factors govern patterns of biodiversity. The criteria determining local coexistence in close relatives have typically been, for ecologists, whether these species meet conditions of stable coexistence when competing for resources; in contrast, evolutionists often consider coexistence of close relatives from the perspective of complete reproductive isolation. Clearly, both of these conditions must be met, but for coexistence in ecologically and phenotypically similar close relatives to occur, species must overcome a diverse suite of challenges beyond just these. The goal of this review is to present a more holistic, eco-evolutionary view of the factors governing successful coexistence of close relatives, expanding our consideration to recent clade mates, not just sister taxa, and drawing on new technologies and approaches to explore more deeply this classic conundrum. We review the major concepts explaining patterns of coexistence in close relatives, distinguishing between forces related to (*a*) history, speciation, and extinction; (*b*) divergence, dispersal, and drivers of range overlap; and (*c*) successful ecological coexistence of species once in contact. We end by highlighting major gaps and ways forward, including moving beyond the strict dichotomy of local and regional scales and scrutinizing

non-native introductions as analogs of secondary contact to tease apart factors contributing to coexistence in real time. By reviewing literature from both ecological and evolutionary perspectives, we hope to illustrate the multifaceted factors that drive coexistence of close relatives and to highlight new questions and approaches that might expand this age-old topic to nonsister close relatives, which often face similar challenges to coexistence as those faced by sister taxa.

## 1. INTRODUCTION

Disentangling the factors that shape coexistence of close relatives is a fundamental problem in ecology and evolutionary biology, one that lies at the nexus of speciation history, ecological niches, and behavior. Factors promoting or impeding coexistence in close relatives shed light on fundamental questions like: What governs community invasibility, what drives latitudinal diversity gradients (LDGs), and what are the mechanisms of speciation? As Darwin (1859) recognized, a fundamental duality is caused when species are relatively recently diverged from one another. On the one hand, the biological similarity and geographic origins of closely related species can promote their co-occurring in the same habitats. On the other hand, close relatives can ecologically, genetically, and reproductively interfere with one another owing to their morphological and ecological similarities. The centrality of this topic has led to a long and rich history of research touching on the drivers of coexistence in close relatives, including the study of limiting similarity and character displacement (e.g., Brown & Wilson 1956, Hutchinson & MacArthur 1959, MacArthur & Levins 1967), species:genus ratios (e.g., Elton 1946), island radiations (e.g., Losos & Ricklefs 2009), hybridization and reinforcement (e.g., Coyne & Orr 1989), and community phylogenetics (e.g., Cavender-Bares et al. 2009, Godoy et al. 2014). Although these different research programs have been immensely fruitful, they have also largely progressed independently of one another. For example, community ecology generally excludes the deeper phylogenetic history of species pools, ignoring historical biogeography [see critiques by Cornell & Harrison (2014), Mittelbach et al. (2007), Ricklefs (2007)]. Alternatively, evolutionary studies of coexistence have focused on speciation, reproductive isolation, and gene flow among close relatives (e.g., Coyne & Orr 1989), ignoring the ecological processes that actually allow populations of species to have stable or positive population growth in sympatry. Thus, for ecologists, local coexistence in close relatives has been dependent on whether species meet the conditions of stable coexistence when competing for resources (e.g., Adler et al. 2007, Chesson 2000), whereas evolutionists consider coexistence of close relatives as dependent on successful reproductive isolation, typically of sister taxa (Schemske 2010). Clearly, both of these conditions and others must be met, though their relative impacts and importance are rarely considered together in a single framework.

The goal of this review is to present a more holistic view of the historical, evolutionary, and ecological factors that govern patterns of coexistence of close relatives (see sidebar, Definitions). We structure our review by distinguishing between forces related to (a) speciation and extinction; (b) divergence, dispersal, and drivers of range overlap; and (c) successful ecological coexistence of species once in contact (**Figure 1**). Modern techniques make this an apt time for such a synthesis. Genomics, phylogenetic advances, better global positioning systems (GPS) monitoring, DNA barcoding, and stable isotope analyses of niches have allowed us to better understand the timing of speciation and species contact, quantify niches as never before in sympatry and in allopatry, and explore trait and niche evolution over time and in the presence and absence of close relatives. All these techniques inform the diverse processes that enable or prevent coexistence.

## DEFINITIONS

*“Close relatives.”* To date, the greatest amount of attention on coexistence in close relatives has focused on sympatry in sister taxa. Because sisters are one another’s closest extant relatives, their study can be particularly useful in understanding the speciation process and the ecological conditions that foster or impede local sympatry. However, interactions with closely related, nonsister clade mates can be as or more important. Here, we define close relatives loosely as relatively recently diverged, morphologically, and/or ecologically similar species. In practice, these species often fall at the taxonomic level of congeners. However, because genera differ in their evolutionary ages, the general principles discussed here are not restricted to a particular depth of phylogenetic relatedness or ecological similarity. Rather, disentangling the complex continuum of phylogenetic and phenotypic distances over which processes shape coexistence across clades is one of the major goals we highlight in the field.

*“Coexistence.”* Coexistence requires nuanced consideration of spatial and temporal scale, migration/phenology, and microallopatry (Siepielski & McPeck 2010). In this review, we define coexistence operationally as the state in which populations of species can maintain long-term positive or equilibrial population growth within dispersal distance of one another. We do not distinguish among the terms sympatry, syntopy, and coexistence. However, we note that microallopatry could qualify as coexistence under this definition, if gametes or organisms can easily disperse between habitats.

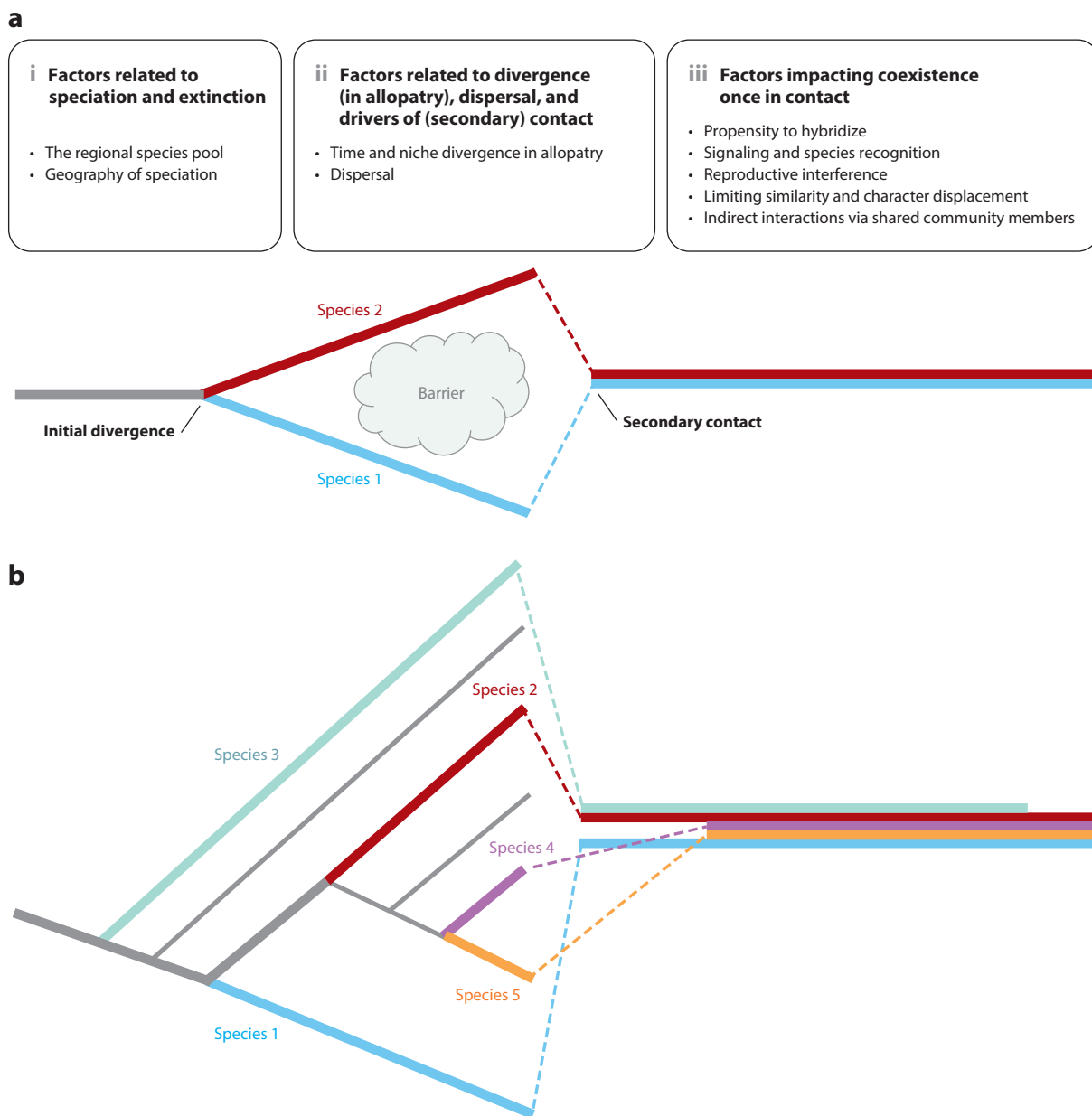
## 2. FACTORS RELATED TO SPECIATION AND EXTINCTION

Speciation and extinction can have prominent roles in shaping patterns of coexistence in close relatives. In this section, we address (*a*) how speciation and extinction shape the composition of the regional species pool and (*b*) how the geography of speciation and the timing of sympatry affect null expectations of coexistence in close relatives. Another contribution in this volume by Stroud & Losos (2016) explicitly explores the role of ecological opportunity in shaping patterns of diversification; thus, the role of ecological opportunity in promoting coexistence in close relatives is not extensively discussed here.

### 2.1. The Impact of Speciation and Extinction on the Composition of Close Relatives in the Species Pool

Patterns of coexistence at their foundation are shaped by the evolutionary history of the regional species pool (Ricklefs 1987). Closely related taxa must occur regionally if they are to coexist locally, and the regional composition of taxa is driven by dynamics of speciation, extinction, and dispersal. Below, we discuss how factors related to speciation and extinction impact expectations for coexistence among close relatives (dispersal is discussed in Section 3).

**2.1.1. Time and area.** A null explanation for why certain groups have higher regional richness (and thus a higher density of close relatives) is time: A group may have more potential for coexistence among close relatives simply because that lineage has been present in that area for a longer amount of time. Time is a strong predictor of both endemism and richness in isolated habitats in both mainland and island settings (MacArthur & Wilson 1967). Evidence for the role of time across larger spatial scales has also been found: Fine & Ree (2006) found strong positive correlations between contemporary species richness and the time that a biome has been present over deep history (accounting for area). Correlations were especially strong and consistent when using a



**Figure 1**

Patterns of coexistence in close relatives are shaped by a suite of evolutionary and ecological factors. (a) Categories of factors implicated in shaping patterns of coexistence among close relatives discussed in this review. The categories are roughly organized along a continuum of time, from the speciation process occurring early in the history of a species pair to long-term successful ecological coexistence once species have achieved full reproductive isolation in sympatry. (b) Although these factors are frequently investigated for sister species, they are important for closely related, nonsister taxa as well, although complexity increases with increased phylogenetic inclusion.

time interval that included the Eocene tropical maximum. The authors concluded that biome area integrated through evolutionary time is the primary predictor of the current latitudinal gradient in tree diversity. Time and area have also been integrated with factors to predict regional richness. Armitage (2015) experimentally demonstrated that, for a given area, time-integrated productivity explained patterns of diversity in *Pseudomonas*. Although time is an important factor to include in null predictions of regional richness patterns, it is not always a strong predictor of patterns of diversity. Extreme variation in the relationship between richness and age exists at the clade level, to the point that clade age and richness are decoupled across major swaths of the tree of life (e.g., Rabosky et al. 2012). This decoupling also plays out in recent phylogenetic studies of diversity gradients, which point to tropical diversity resulting from both cradle dynamics, fostering more speciation, and museum dynamics, in which lineages fail to go extinct (Moreau & Bell 2013). Together, these results suggest that time alone cannot be assumed to be the primary predictor of species richness in most clades and that additional factors must be considered.

**2.1.2. Extrinsic factors.** Many extrinsic conditions have been implicated in promoting diversity at the clade level (Heard & Hauser 1995), thereby facilitating greater incidence of close relatives in certain regional species pools relative to others. External factors such as resource availability (e.g., Wagner et al. 2012), climate (e.g., Crisp et al. 2004), habitat heterogeneity (e.g., Price et al. 2011), predation regime (e.g., Vamosi 2003), habitat isolation (e.g., MacArthur & Wilson 1963), habitat size/area (e.g., Kisel & Barraclough 2010), and existing species diversity (e.g., Losos 2010) have all been implicated in shaping patterns of clade richness. In many cases, these external drivers have been studied in radiations on islands or island-like systems such as mountaintops or lakes (Losos & Ricklefs 2009), though mainland dynamics with their diverse communities may not be accurately described by island speciation mechanisms. Specifically, in the context of more diverse communities, there may be fewer empty niches into which resident taxa can radiate (Stroud & Losos 2016, Rabosky & Hurlbert 2015). Both the LDG and the evolving metacommunity literature point to extrinsic factors in shaping diversity (Pigot et al. 2016, Urban et al. 2008). Pigot et al. (2016) found that, globally, higher productivity regions were associated with greater rates of local sympatry in bird sister taxa. Whether this pattern arises from more resources that allow sisters to coexist, from less extinction by sister taxa because of increased resources, or from less hybridization/reproductive interference/habitat partitioning by sister species in more architecturally diverse habitats is unknown. It would be interesting to see whether the same relationship between productivity and greater incidence of sympatry extends to close relatives beyond sister taxa and at which spatial and phylogenetic scale these patterns begin to break down.

**2.1.3. Intrinsic factors.** Many intrinsic factors (i.e., lineage-specific traits) are also hypothesized to play an important role in determining the diversity of clades and thus their potential for representation in the regional species pool. Sexual selection and sexual conflict (e.g., Panhuis et al. 2001), ecological specialization (e.g., Farrell 1998), reproductive traits (e.g., Hodges 1997), ecological versatility (e.g., Liem 1973), spatial vagility/dispersal ability (e.g., Claramunt et al. 2012), and defensive traits (e.g., Weber & Agrawal 2014) have all been implicated in shaping patterns of richness. These traits should be considered when developing null expectations for coexistence patterns among groups, as their presence alone may impact local coexistence by enhancing or squelching diversity of a clade at the regional scale. Patterns can be confounded if traits also have impacts on ecological interactions between close relatives or on trait-facilitated habitat filtering. Future work that simultaneously examines how intrinsic traits shape coexistence among close relatives at both phylogenetic and ecological scales will be insightful.

Most studies of intrinsic factors have focused on radiations, but it is also well worth considering species or groups that have failed to diversify [depauperons in the parlance of Donoghue & Sanderson (2015)] even when these depauperons have occupied the same habitats and areas for equal amounts of time as clades undergoing extensive diversification. Depauperon cichlid lineages in African rift lakes tend to lack sexual dichromatism compared with their radiating counterparts (Wagner et al. 2012). It is important to note, however, that in a given region some clades may fail to radiate not because of intrinsic traits but because they arrived at that region after available niche space had already become occupied by other taxa. Using time-calibrated phylogenies, Tanentzap et al. (2015) integrated paleoclimatic and paleogeological perspectives to reconstruct occupancy of environmental space through time across 16 genera in New Zealand. They found that earlier-colonizing lineages displayed greater species diversity, greater occupancy of niche space, and subsequently more dominance in local communities, supporting the hypothesis that early radiations can reduce niche availability and dampen diversification of later arrivals.

Few studies have simultaneously investigated the relative roles of intrinsic versus extrinsic factors in shaping contemporary patterns, but those that have consistently find that both types of factors interact to drive patterns of clade divergence. In a study by Wagner et al. (2012), a combination of extrinsic environmental factors related to ecological opportunity (lake depth and available energy) and intrinsic lineage-specific traits related to sexual selection (sexual dichromatism) was required to predict whether cichlid lineages radiated or not across 46 African rift lakes. In plants, Drummond et al. (2012) found that increased speciation rates in *Lupinus* required both the evolution of a perennial lifestyle and movements into montane habitats. In a more broad study of major angiosperm clades, Bouchenak-Khelladi et al. (2015) found not only that, across Ericaceae, Fagales, and Poales, radiations required both intrinsic and extrinsic drivers to occur but also that the specific sequence of these events was not important. Donoghue & Sanderson (2015) introduced the term synovation to describe interactions among factors in diversification. Beyond just identifying interactions among factors, drivers of regional clade diversity ultimately need to be fully integrated into studies of coexistence rather than treated as a distinct field [see reviews by Mittelbach & Schemske (2015), Mittelbach et al. (2007), Ricklefs (1987), Wiens (2011)]. One important step in this process will be linking these drivers of clade diversity to regional diversity, a task that will require the integration of fine-scale historical biogeography with phylogenetic comparative studies of diversification rates. Recent innovations in dating molecular phylogenies paired with biogeographical analyses are now allowing for a more accurate picture of the order of arrival of different taxa into regional species pools (e.g., Tanentzap et al. 2015), an approach that is on the cutting edge of linking ecology and evolution to study contemporary coexistence among close relatives.

## 2.2. Geography of Speciation

The geography of speciation can directly and indirectly impact coexistence in close relatives. In this section, we briefly discuss the ways in which different speciation modes can influence the probability that closely related species will coexist. For simplification, we separate our discussion into the three classic categories of speciation (sympatric; para- and peripatric; and allopatric), but we recognize that these distinctions are a somewhat artificial discretization of what is more realistically a continuum of speciation scenarios.

**2.2.1. Sympatric speciation.** Arguably, the most relevant phenomenon to coexistence in close relatives is sympatric speciation, as its very occurrence inherently includes the overlap of recently speciated taxa. The prevalence of sympatric speciation is thought to be low, but when successful

it results in immediate coexistence of sister pairs (Bolnick & Fitzpatrick 2007). For example, polyploid speciation events are immediate, and subsequent hybridization is low to absent owing to chromosomal incompatibility (e.g., Crawford & Rudgers 2012, Hanzl et al. 2014). Aside from cases of ploidy change, sympatric speciation has been implicated in cichlids, island palms, phytophagous insects, and sexually selected organisms (Barluenga et al. 2006, Berlocher & Feder 2002, Higashi et al. 1999, Savolainen et al. 2006, Via 2001). Because sympatrically speciating taxa have a head start in terms of their timeline for potential range overlap, the likelihood of sympatric speciation should not be ignored as a potential explanatory factor in studies explaining patterns of coexistence in close relatives. However, without the time and space to ecologically or reproductively diverge that are afforded by other speciation modes, sympatrically speciating pairs, once formed, may face greater hurdles coexisting. Little is known about the proportion of sympatrically speciating lineages that are able to maintain coexistence long term and, conversely, how many sympatrically speciating taxa have gone extinct owing to ecological exclusion of one species by the other.

**2.2.2. Para- and peripatric speciation.** Similar to sympatrically speciating groups, clades that speciate para- and peripatrically should also be more likely to experience coexistence sooner than allopatrically coexisting groups simply by virtue of the geography of their speciation mode. Para- or peripatrically speciating groups may also face increased hurdles to downstream coexistence owing to the short timescales for ecological divergence in allopatry. Although allopatric speciation is considered the norm in animals, age-range correlations (ARCs) suggest that para- or peripatric speciation may be common in plants. For example, ecological similarity, range overlap, and range asymmetry were related to time since divergence of 71 plant sister species pairs in the California Floristic Province (CFP) (Anacker & Strauss 2014). Sisters in the CFP were at least partially sympatric in 80% of cases, and range overlap and range size asymmetry were greatest in younger sisters. These results suggest budding or peripatric speciation, in which a larger-ranged progenitor gives rise to a smaller-ranged derivative species (see also Barraclough & Vogler 2000). Speciation in peripatry and sympatry may be enabled by the increased incidence of ploidy shifts or self-fertilization in plants versus animals or by single mutations of large effect that can quickly result in reproductive isolation via pollinator shifts (e.g., Bradshaw & Schemske 2003; but see also Givnish 2010 for review). In accordance, greater sympatry was found in outcrossing-selfing *Mimulus* sister pairs than in outcrossing pairs (Grossenbacher & Whittall 2011); however, this result did not hold over a larger diversity of Californian genera (Grossenbacher et al. 2015).

**2.2.3. Allopatric speciation.** Allopatric speciation is considered by far the most common mode of speciation. Allopatrically speciating taxa may fail to coexist simply owing to biogeographic or historical factors. With millions of years frequently elapsing prior to secondary contact (Fitzpatrick et al. 2009), other factors need not necessarily be invoked to explain a lack of ecological coexistence. Some studies account for the influence of allopatric speciation on the likelihood of coexistence in close relatives by limiting the species they are investigating to only those that are close enough in time and space that they could come in contact with one another (e.g., Cardillo 2012). However, determining the relevant spatial proximity for potential interactions can be challenging, as dispersal limitations can operate at small spatial scales owing to factors such as habitat heterogeneity. A more seamless integration of historical biogeography into studies of contemporary coexistence could help inform when and where species pairs are truly isolated allopatrically and can be safely omitted from downstream analyses.

Because speciation mode itself directly impacts the probability of coexistence in close relatives, ideally studies should explicitly test for signatures of speciation history when attempting to disentangle mechanisms driving nonrandom patterns of coexistence (Warren et al. 2014). This has



been attempted using several approaches, perhaps the most rigorous of which is to apply a full phylobiogeographic framework to reconstruct the history of populations both within and across species involved in the study (e.g., Pettengill & Moeller 2012). Although biogeographical analyses can directly evaluate the likelihood of speciation histories leading to contemporary patterns of coexistence, they can also be prohibitively difficult to accomplish rigorously, especially in groups with limited geographic information. A more common, but also more assumption laden, approach is to apply ARCs (Barracough & Vogler 2000, Warren et al. 2014), in which time since divergence in species is regressed against range overlap. For example, studies of beetles and plants using ARCs show evidence for peripatric speciation (Anacker & Strauss 2014, Barracough & Vogler 2000). A similar framework examines the age and niche divergence of just sister pairs with range overlap compared with pairs with no range overlap. For example, Tobias et al. (2014) used sister species to show that closely related pairs of oven birds with overlapping ranges are on average 2.3 times older than those with no range overlap, suggesting a dominant mode of allopatric speciation with secondary contact. In both ARC and sister-pair comparisons, range asymmetry can also add to information on the process: Much greater range size disparity in young versus older sister pairs was found in both plants and beetles, suggesting that budding speciation is likely the dominant mode. However, although these approaches are popular, recent work has suggested that both ARC (Warren et al. 2014) and sister-pair (Pontarp et al. 2015) studies should be interpreted with caution, as inferring the geographical speciation mode from just phylogenies and the biogeography of extant species may be impossible in many cases. Also, variation in both range overlap and asymmetry may reflect variation in dispersal abilities among taxa rather than differences in speciation modes. It may be that because plants are sessile, their geographic distributions may be slower to expand than those of animals, whose vagility may make it harder to infer speciation processes from ARCs and current geographic overlap.

### 3. DIVERGENCE OF THE NICHE, DISPERSAL, AND DRIVERS OF RANGE OVERLAP

#### 3.1. Time, Trait Divergence, and the Erosion of the Fundamental Niche in Allopatry

Although literature on coexistence is often focused on character displacement in sympatry, it is equally important to consider lineage divergence during allopatry, especially given that allopatric speciation is the primary mode of speciation for many clades. The amount and type of divergence in allopatry can have direct implications for downstream coexistence dynamics in close relatives (Pearman et al. 2008). For example, if coexistence at secondary contact is prevented by ecological competitive exclusion, close relatives that are more diverged at the time of secondary contact should be more likely to successfully coexist (Tobias et al. 2014). Alternatively, in clades in which local coexistence is driven primarily by environmental filtering, divergence in allopatry should decrease the probability of local coexistence in close relatives, as niches and habitat preferences diverge. Explicitly integrating divergence in allopatry into studies of coexistence is an important step toward identifying mechanisms driving contemporary community composition and regional species pools.

How does one quantify the amount of divergence that has accrued in allopatry? This requires quantifying (*a*) the time since divergence (species pair age) and (*b*) the rate of evolution in the relevant niche axes. Phylogenetic studies using environmental niche models aim to quantify the amount of niche differentiation as a function of time since divergence and range overlap (Peterson 2011). In one example, Warren et al. (2008) used a form of this approach to disentangle



geographic and niche overlap in Cuban anoles. They found that environmental niche overlap was positively associated with geographic overlap rather than predicted by phylogenetic distance, and they concluded that phylogenetic niche conservatism has not been a major factor constraining local coexistence of closely related species. Although environmental niche models are helpful, there is still debate over what aspects of the niche these models actually reflect and whether those aspects are relevant for ecological coexistence (Godsoe 2010).

Similar to environmental niche modeling, macroevolutionary studies of trait evolution also aim to describe the rate and nature of divergence across close relatives using phylogenetic models of character evolution, often focusing on traits relevant for coexistence. However, few comparative phylogenetic studies explicitly incorporate allopatry into models of trait evolution, largely because of challenges associated with reconstructing coexistence back through time in comparative analyses. Progress is being made in this arena: The development of ancestral range reconstruction methods is an active area of research (e.g., Landis et al. 2013, Matzke 2013). Many studies sidestep this issue by focusing on sister-pair studies rather than by using whole-clade perspectives. Reconstructing range overlap in a single pair of very recently diverged taxa requires far fewer assumptions than reconstructing range overlap of many closely related species (a whole genus, for example) over their entire evolutionary trajectory. Using sister species allows one to ask, for example, whether coexisting species pairs are more divergent than expected based on time since their initial speciation (i.e., more time has elapsed in allopatry for divergence to take place) or because of elevated evolutionary rates once species experience range overlap (i.e., rapid divergence via character displacement upon secondary contact). A test of this idea was done using an extensive 350-lineage radiation of insectivorous ovenbirds that has occurred over 35 My. Tobias et al. (2014) measured divergence in two key functional traits associated with resource competition and territoriality (beaks, tarsi, and song) between closely related species pairs that were sympatric or allopatric. Although sympatric lineages had significantly greater overall trait divergence than allopatric lineages, once evolutionary age of the pair was taken into account, divergence in beaks and tarsi was no longer greater than expected. That is, the divergence was due to the older age of sympatric pairs rather than an increased rate of trait evolution. Interestingly, song remained more diverged than expected.

A completely different approach to quantifying the erosion of the niche over evolutionary time is experimental, taking advantage of the fact that sessile species can be transplanted and forced to live in the niches of other species. Anacker & Strauss (2016) explored this question by transplanting 14 species into the field niches (dense patches) of species that varied in their phylogenetic relatedness to the focal planted species. Over 2 years and across different sites, performance was consistently nonlinearly related to divergence time. Species performed best in conspecific patches, with declining performance at sites where the resident was <65 My diverged, whereas at sites where the resident was >65 My diverged, performance increased to that at conspecific sites. Biotic interactions with close relatives, as well as with enemies like soil pathogens or herbivores, which often have affinities for plant hosts up to the family level, may also play a part in observed niche erosion patterns (see also Ricklefs 2015, Rohr & Bascompte 2014, Terborgh 2015, Webb et al. 2006). In the example above, half of the transplants also received neighbor removals to separate effects of soil biota alone and other abiotic factors from direct interactions. A linear negative relationship between time since divergence of the focal and neighbor species and the degree of suppression was found: Congeners suppressed growth more than confamilials, and distant relatives were neutral to facilitative, results suggesting attrition of ecological similarity over time. Consistent with these experimental results, observational data on fine-scale spatial associations showed spatial repulsion and reduced ecological coexistence among native congeners in the community.

### 3.2. Dispersal

Dispersal has long been a central concept in the study of coexistence. Research on metacommunities, biogeography, and community ecology suggests that dispersal ability is a critical factor in determining regional coexistence of species. But how is dispersal relevant for determining coexistence among close relatives, *per se*? Dispersal ability itself can have a strong phylogenetic signal, as it is mediated by heritable traits in many systems. For example, a study of 330 understory forest plants found that closely related species were more similar to one another in their ability to colonize postagricultural forests than were distantly related species (Baeten et al. 2015), and a study across mammals found high phylogenetic signal in both maximum and median dispersal distance (Whitmee & Orme 2013). This conservatism in dispersal ability could translate into nonrandom patterns of coexistence among close relatives in several possible ways. In allopatrically speciating clades, groups with high dispersal abilities should experience secondary contact sooner than clades with low dispersal abilities (as well as faster reduction in any range asymmetries over time). One result might be decreased rates of coexistence in high dispersing lineages, if not enough time before secondary contact has elapsed for sufficient ecological niche divergence. In addition, if dispersal ability is too high, speciation rates may be low owing to increased gene flow/hybridization (see Claramunt et al. 2012 for an example in migrating birds).

Evolutionary lability and variation in dispersal traits among close relatives can be mechanisms for coexistence through a range of different processes. For example, variation in densities of species due to dispersal abilities can increase coexistence rates [e.g., decreasing spatial aggregation (Potthoff et al. 2006) and increasing competition with conspecifics (Salomon et al. 2010)]. The role of dispersal variation was investigated using simulations of communities of fish on the Great Barrier Reef, where Bode et al. (2011) found that variation in dispersal ability among species was, by itself, sufficient to achieve successful coexistence. Extending this theory to a phylogenetic perspective would suggest clades with conservatism in dispersal-related traits should be at a disadvantage for coexistence, whereas those that diversified rapidly in dispersal traits may be more likely to coexist.

The evolving metacommunity literature also suggests relationships between dispersal and coexistence. As species disperse into an area, they may usurp niche space and reduce the ability of other species to colonize or of residents to radiate into new niches (Urban et al. 2008). Thus, coexistence in close relatives via adaptive radiation may be reduced in the presence of dispersal and colonization by other species that are better able to use those resources. Such dynamics have been predicted in models (De Mazancourt et al. 2008) and shown in micro- and mesocosm experiments (Fukami et al. 2007, Pantel et al. 2015). For bacteria, when an ancestral genotype was introduced into a spatially diverse habitat, it diversified into multiple niche-specialist types (Gomez & Buckling 2013). However, if these habitats were colonized by a niche specialist relatively soon after the introduction of the founding bacterium genotype, diversification in the founder bacterium was suppressed. These models suggest that coexistence in close relatives reflects a race between *in situ* speciation in novel heterogeneous environments and colonization by new species that are better able to use those niches (Urban et al. 2008).

## 4. FACTORS AFFECTING SUCCESSFUL COEXISTENCE ONCE IN CONTACT

In *The Origin of Species*, Darwin wrote: “As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera” (Darwin 1859, p. 79). Although Darwin’s thoughts were

framed by the struggle for resources, once species have reached the same area, successful ecological coexistence in close relatives depends on a large number of processes beyond just competition. In the following sections, we explore the consequences of similarity in close relatives for coexistence in terms of the diverse suite of hurdles taxa experience once they come into contact.

#### 4.1. Limiting Similarity, Competition, and Niche Divergence in Sympatry

The classic explanation for why we see coexistence in close relatives focuses on niche divergence in sympatry and the reduction of limiting similarity; however, major questions about how, when, and where limiting similarity shapes patterns of coexistence in close relatives remain open, despite the length of its tenure in ecology.

Recent models predict that coexistence is a function of two species properties: fitness differences (a.k.a. equalizing effects) and niche differences (a.k.a. stabilizing effects) (Adler et al. 2007, Chesson 2000). Specifically, the more diverged two niches are, the more species can differ in their fitness and still successfully coexist. Ample evidence exists that many aspects of niches are phylogenetically conserved, but much less information exists on the degree of conservatism in equalizing effects (i.e., how conserved are fitness differences). For example, propagule packaging might be one fitness trait that is relatively labile, yet empirically, studies of coexistence frequently treat fitness as total biomass of progeny and are agnostic as to packaging (Godoy et al. 2014). With conserved niche differences (causing intense competition predicted between relatives) and conserved fitness differences (causing near neutrality and ecological equivalence) in close relatives, coexistence depends on the relative strength of these opposing forces (Anacker & Strauss 2016, Godoy et al. 2014, Siepielski & McPeck 2010).

Although newer theory includes both fitness and niche differences, the classic framework for studying coexistence was focused on limiting similarity and stabilizing forces, revolving primarily around quantifying niche differences (Elton 1946, MacArthur & Levins 1967). New tools are getting us closer to measuring most of the  $n$ -dimensions of the stabilizing forces of niche divergence. The plains and Grevy's zebras, which often graze in mixed herds in sympatry and mainly eat grass, would seem to share identical niches. However, DNA barcoding of dung found 14 grass species and a forb species that separated their diet niches in multivariate diet space. That said, far more plants were shared by both zebra species, and plains zebra diets overlapped almost completely with those of the Grevy's zebras (Kartzinel et al. 2015).

Our tendency is to be happy when we can document any niche difference, and most studies assume that measured differences might be sufficient to explain coexistence of two species. Sometimes, however, new tools show little to no niche differentiation between close relatives [e.g., 15 syntopic *Monomorium* ant spp. (Andersen et al. 2013) and flycatchers (Botero-Delgadillo 2011, Mason & Taylor 2015)]. The neutral theory of community assembly assumes that many species in local communities are ecologically equivalent and that species occupancy depends on local densities and dispersal (Hubbell 2001). At the phylogenetic scale of close relatives, niche equivalency and neutral dynamics may be common. Few studies explore the relative magnitude of suppression by conspecifics and congeners toward that aim (e.g., Anacker & Strauss 2016, Burns & Strauss 2011, Siepielski & McPeck 2013). Some of the best tests of niche equivalency have been conducted using field experiments on damselfly communities of three syntopic genera. For all genera, intergeneric competition was low and intrageneric competition was high; among species in the genus *Enallagma*, especially, no differences in strength between intrageneric and conspecific competition were found (Siepielski et al. 2011). Natural distributions of damselflies across lakes are consistent with neutral or nearly neutral models, suggesting niche equivalency in congeners.

Longer-term field studies and experimental removals allow for the comparison of fundamental niches with and without congeners. On Scandinavian islands, the coal tit (*Parus ater*) often occurs with two other congeners. When congeners are absent, *P. ater* can markedly change body size (a heritable trait) and take over the foraging niche of the other species (Norberg & Norberg 2015), again suggesting latent niche equivalency. Although species removals could indicate the degree to which close relatives are suppressed by each other, ghosts of interactions past can reduce the effects of neighboring species, at least over the short-term scales of ecological experiments. Results have been mixed. In many examples of congeneric removals, remaining congeners have increased in population size and altered resource use, expanding their niche to use the resources previously usurped by the other species—for example, antbirds in Panama (Tobias as cited in Norberg & Norberg 2015), Galapagos finches (Grant & Grant 2006), and coal tits in Sweden (Norberg & Norberg 2015). In some cases, like antbirds, we can see these effects immediately—one species of antbird replaced the other when the resident territory holder disappeared (Tobias as cited in Norberg & Norberg 2015), suggesting great niche equivalency in close relatives. A lack of response suggests either no competition or longer experimental time periods may be required before remaining relatives use freed resources. It may take time for natural selection to act on rare but existing genetic variation that allows niche expansion. This speed may also be influenced by plastic or transgenerational effects on expression of the niche (Mason & Taylor 2015). Regardless, natural or devised experiments of congener removal often reveal that, yes, close relatives compete strongly (Anacker & Strauss 2016, Jankowski et al. 2010) and, strikingly, closely related species can consistently take over the niches of their congeners.

Another key issue in the study of limiting similarity is predicting when competition among close relatives leads to trait divergence. Several studies predict that an outcome of competition is not phenotypic divergence in sympatry but rather convergence, whereby competing for the same resources can cause species to converge on similar traits (Abrams 1996, Miller & Moran 2014). The circumstances under which competition is predicted to drive trait convergence or divergence depend on resource availability and ecological opportunity: Convergence is predicted in cases of strong competition for a limiting and rare resource with no alternatives, whereas divergence is predicted in cases where resource alternatives are present (Fox & Vasseur 2008). The jury is out on how often resource competition between close relatives is the driving force causing niche divergence when species come into contact. In the next section, we discuss how other forces related to reproduction may drive niche divergence and coexistence of close relatives in the absence of resource competition.

## 4.2. Propensity to Hybridize

Reproductive isolating mechanisms clearly play an important role when close relatives come into contact. Mechanisms preventing hybridization that initially allowed speciation in parapatry can be lost or may be nonexistent if speciation occurred in allopatry. Any resulting hybridization at secondary contact can select for increased reproductive isolation (reinforcement) (Hudson & Price 2014, Servedio & Noor 2003), often through habitat segregation (e.g., Anacker & Strauss 2014), or cause the collapse of species in contact areas (Abbott et al. 2013). All of these forces can reduce coexistence.

Although hybridization as described above is thought to collapse incipient speciation, it can also spur radiations by introducing large amounts of new phenotypic variation on which selection can act, thereby generating new opportunities for niche partitioning and subsequent coexistence in sympatry by close relatives (Abbott et al. 2013). Hybridization events have been implicated as important in our most iconic sympatric radiations—from Galapagos finches (Grant & Grant

2002, Lamichhaney et al. 2015) to cichlids (Seehausen 2015, Stelkens et al. 2015). Heterospecific matings may also occur more often than recognized (Cothran 2015, Rohde et al. 2015), especially between phenotypically similar sympatric close relatives (e.g., Drury et al. 2015a). One study on interspecific territoriality (IT) in warblers showed greater IT in syntopic, more closely related, and more phenotypically similar species; these species were also more likely to extensively hybridize (3/19 IT species pairs versus 0/286 non-IT pairs; see Grether et al. 2009). These heterospecific matings may ultimately be an important driver of sympatric speciation, or at least coexistence, by increasing phenotypic variation on which selection can act (Abbott et al. 2013, Grant & Grant 2002).

### 4.3. Shared Signals Can Both Impede and Promote Local Coexistence in Close Relatives

Even when species are completely reproductively isolated, signaling and species recognition dynamics can influence local coexistence of close relatives. Species recognition, the behavioral discrimination between conspecifics and heterospecifics (Mendelson & Shaw 2012), serves many purposes, including individual mate recognition, recognition of neighbors in territorial animals (e.g., Grether 2011), antipredator behavior and mutualistic interactions like shared alarm cues (e.g., Dalesman et al. 2007, Hazlett & McLay 2005, Mitchell et al. 2012), mixed species mobbing and defense (e.g., Goodale et al. 2010), and mixed species foraging and use of shared resources (e.g., Symonds & Wertheim 2005). In animals, species recognition is often based on color, chemical communication, or vocalizations (Pfennig & Pfennig 2012). Plants use many of the same types of signals—roots respond to chemical cues of kin, heterospecific neighbors, and conspecific neighbors (Dudley et al. 2013); volatile chemicals can communicate within and across other plant species (e.g., Karban et al. 2000); and colors serve to attract animal species that provide mating opportunities or dispersal (e.g., Hopkins & Rausher 2012, Moeller & Geber 2005).

Despite the importance of species recognition, evidence that animals frequently cannot or do not distinguish between conspecifics and closely related heterospecifics has been found (Ord & Stamps 2009). Owing to phenotypic and cognitive similarity through shared ancestry, signals may be more similar in close relatives, a prediction supported by the greater incidence of heterospecific interactions among close relatives (Mitchell et al. 2012, Peiman & Robinson 2010). Additionally, close relatives often share phylogenetically conserved cognitive and behavioral responses to each other's signals (Grether 2011)—for example, sharing/recognizing predator alarm calls or aggregative cues promoting resource utilization, as described above. This similarity in signal and signal response in close relatives can directly impact coexistence, both positively and negatively.

**4.3.1. Similarity in signals promotes coexistence.** Selection may favor similar responses to heterospecifics and conspecifics (e.g., Symonds & Wertheim 2005). Signals may converge (or not diverge) if there are advantages to colocation and communication, such as shared predator defense (Dalesman et al. 2007, Mitchell et al. 2012), fostering increased densities of shared mutualists (Moeller & Geber 2005, Sargent & Ackerly 2008), or increasing the efficiency of resource use through communication (e.g., aggregative pheromones of *Drosophila* spp.; see Symonds & Wertheim 2005). In all of these examples, close relatives tend to exhibit these interspecific behaviors most, and ample evidence (from snails, crabs, fish, bats, birds, and more) shows that both cues and appropriate responses to them are phylogenetically conserved (e.g., Peiman & Robinson 2010). In one striking example, bird migrants increased rates of territory establishment near playback calls of closer relatives; only phylogenetic relatedness, not multivariate niche or diet, predicted responsiveness to playbacks (responsive species averaged 9.01 million years diverged,

whereas unaffected species were 55 million years diverged (DeJong et al. 2015). In this way, fitness advantages to conserved cosignaling may favor coexistence in close relatives.

**4.3.2. Signal similarity impedes coexistence.** If fitness is reduced by inappropriate responses to heterospecific signals, signals will diminish local coexistence in close relatives—for example, if species unnecessarily defend resources against heterospecifics or mistake heterospecifics for mates (e.g., Drury et al. 2015b). Fitness-reducing heterospecific interactions through signaling are hypothesized to be strongest when species first encounter each other through range expansions. Although these dynamics are considered transient, several recent studies have suggested that the effects of heterospecific signaling interactions on local coexistence persists for long periods of time (Drury et al. 2015a, Losin et al. 2016). IT in wood warblers occurs primarily and consistently between closely related, sympatric species that are phenotypically similar in plumage and song (Losin et al. 2016); heterospecific matings often result in hybridization (Rohde et al. 2015) or reduced fitness (e.g., Runquist & Stanton 2013).

#### 4.4. Reproductive Interference and Coexistence

A less appreciated, but potentially very important, process impeding coexistence of close relatives is reproductive interference (RI). RI is an interaction between reproductively isolated heterospecifics involved in mate acquisition that reduces the fitness of at least one of the species (Groning & Hochkirch 2008). Not surprisingly, RI has been documented most often in close relatives (Groning & Hochkirch 2008, Hochkirch et al. 2007) and impedes coexistence (Drury et al. 2015b). RI has been demonstrated in plants that rely on pollinators for matings, where heterospecific pollen deposition can reduce the area of the stigmatic surface or alter histological responses that reduce the success of conspecific pollen. For example, in *Arenaria* (Fishman & Wyatt 1999), *Limnanthes* (Runquist & Stanton 2013), and *Ipomoea* (Smith & Rausher 2008), competitive interference from heterospecific congeneric pollen transfer imposes fitness costs.

RI is often overlooked as an alternative hypothesis to resource competition in driving ecological niche divergence in clade mates, and several examples now suggest that selective forces driving species to diverge in habitat use are initiated by RI rather than by resource competition (Yamaguchi & Iwasa 2015). Losin et al. (2016) showed that warblers were more likely to exhibit interspecific aggression if they were closely related and phenotypically similar in plumage and song but not if they were similar in ecological traits. Beetle females diverge in resource use in sympatry when heterospecific males are present (Kishi & Tsubaki 2014). A recent model of diversification in herbivorous insects suggests that RI and resource competition are jointly important (Kishi & Tsubaki 2014): Speciation arose commonly when levels of both RI and resource competition were intermediate and seldom if RI was absent.

RI primarily reduces ecological coexistence of close relatives through frequency-dependent processes (Rohde et al. 2015, Runquist & Stanton 2013), and frequency-dependent fitness is a key theoretical condition of ecological coexistence (Chesson 2000). The concept of increase-when-rare (IWR) relies on intraspecific resource competition being stronger than interspecific resource competition (Adler et al. 2007, Chesson 2000, HilleRisLambers et al. 2012); rare invading heterospecifics compete primarily with heterospecifics and gain a competitive advantage because high-frequency residents are most suppressed by competition from conspecifics, allowing the invader heterospecific to IWR. This differential degree of suppression allows heterospecifics to invade patches, fostering frequency-dependent coexistence. However, frequency-dependent impacts of inappropriate matings via RI can reduce the fitness of rare species, obviating the advantages of rarity in resource competition (see above). RI thus reduces coexistence, even when



resource competition is less intense for the rare species. If RI is more important than resource competition in driving coexistence of close relatives, we predict the fitness of a species should decrease as the frequency of congeners or close relatives increases; whereas, under resource competition, the reverse is predicted to be true. These predictions can be tested using manipulations or observations of frequency-dependent fitness (Runquist & Stanton 2013).

#### **4.5. Influence of Indirect Interactions with Shared Community Members on Coexistence of Close Relatives**

Compared with competition, indirect interactions via mutualists and disease have been less considered in studies on the coexistence of close relatives. By altering the facilitation–antagonism balance, interactions with a third player can facilitate coexistence of close relatives in two ways: if the benefit of interactions with a third player is stronger than the cost of negative interactions between congeners or if they act to alleviate direct congeneric competition between species (Callaway 2007, Levine 1999). In addition, interactions with mutualists and enemies are often conserved across genera and even families. Specificity in mutualists (such as microbial mutualists, pollinators, or seed dispersers) can promote coexistence of close relatives by increasing the abundance of specialist mutualists and thus benefitting all closely related species (e.g., Moeller & Geber 2005, Sargent & Ackerly 2008). However, phylogenetic structure in shared enemies can also suppress coexistence of close relatives (e.g., Connell 1970, Janzen 1970, Kursar et al. 2009, Webb et al. 2006). Alternatively, shared antagonists like disease and predators can promote coexistence if shared enemies suppress populations such that resources can support two similar species instead of just one (Terborgh 2015).

In sum, ecological coexistence in close relatives is an emergent property of a large suite of factors. Although resource competition and limiting similarity have traditionally been considered paramount, growing evidence suggests that coexistence in close relatives is especially complicated by the similar phenotypes of closely related species, which can lead to shared enemies and mutualists, RI, and heterospecific interactions that can have large impacts on the ability to coexist locally.

### **5. FRONTIERS IN THE STUDY OF COEXISTENCE IN CLOSE RELATIVES: FUTURE DIRECTIONS**

This is an exciting time to study coexistence in close relatives as boundaries between fields are disintegrating and integration is becoming the norm. New methods are allowing for the incorporation of genomic, phylogenetic, and nuanced ecological approaches. Although we have identified some future directions in the individual sections above, we now identify areas we think are particularly exciting frontiers in the study of coexistence in close relatives.

#### **5.1. Beyond Single-Factor Studies: Simultaneously Studying the Relative Importance of Different Factors in Determining Local Coexistence**

In this review, we hope to have shown that coexistence is clearly a multifaceted phenomenon; however, few studies simultaneously explore the effects of multiple evolutionary and ecological factors in driving local coexistence in a single system.

One major area going forward will be to test the relative importance of resource competition compared with other processes in preventing or allowing local coexistence. Several reasons call into question resource competition as the sole driver of divergence. For example, models suggest

that characters may converge, not diverge, in competition (Abrams 1996, Vasseur & Fox 2011), and state-of-the art niche measurements often show little to no divergence in diets. Additionally, many other organisms, often from different phyla, consume the same resources [e.g., crossbills and squirrels (Benkman et al. 2001); rodents and ants (Brown & Davidson 1977); bees and finches (Schluter 1986)] but are rarely accounted for.

Additionally, growing evidence shows that signaling and RI may contribute to coexistence as much as competition. Both ecological and historical approaches could tease apart these factors. Using historical approaches, comparisons could be made between the rates of evolution of resource acquisition traits and other traits (e.g., sexually selected traits) to disentangle which are evolving more rapidly in sympatry. Another approach would be to ask if coexistence is relatively more likely when at least one close relative in sympatry is largely or completely selfing (Grossenbacher & Whittall 2011, Grossenbacher et al. 2015) or polyploid (Castro et al. 2011, Husband & Schemske 2000) or if co-occurring species are markedly diverged in mating traits such as color patches and pollinator type (e.g., bees and hummingbirds) (Bradshaw & Schemske 2003). Divergence in mating-related traits that is greater in sympatric pairs relative to allopatric pairs of close relatives would support an RI scenario. An ecological approach might explore frequency-dependent fitness in close relatives that are sympatric or peripatric. RI should be greater when one species is at low frequency, with accompanying decreases in fitness (see Section 4). In contrast, resource-based models of coexistence predict high fitness at low frequency through IWR dynamics. Moreover, if close relatives are ecological equivalents (e.g., if resource use is similar), we expect few fitness differences with changes in frequency (e.g., Siepielski et al. 2011).

## 5.2. Relaxing the Strict Binary Division of Local and Regional Scales

The processes driving coexistence have historically been divided between those operating at regional scales and those operating at local scales. In particular, processes like speciation, extinction, and dispersal have traditionally been considered important at the regional scale, whereas processes such as ecological sorting and interactions are generally considered important at the local scale (Mittelbach & Schemske 2015). However, this dichotomy has been criticized as hindering the field's ability to effectively study the drivers of species richness (Ricklefs 2008, Warren et al. 2014). We suggest that this issue is particularly relevant for the study of coexistence in close relatives. In close relatives, dynamics are occurring over shorter periods, often in the same geographic areas. Moreover, because interactions between recently diverged species can have considerable impacts on divergence, feedbacks between evolutionary and ecological processes are possible. Rather than forcing processes into regional or local bins, studies on coexistence in close relatives might be best examined using continuous, but potentially nested, phylogenetic and spatial-scale analyses.

## 5.3. Introduced Species as Modern Analogs for Secondary Contact

Despite the many disadvantages to our moving species around the globe, introductions may provide an opportunity to learn about processes involved in community assembly of close relatives (e.g., Simberloff 1981). Virtually every process influencing coexistence that we discussed above has been documented when an exotic congener was introduced to a local community with a native congener. More recently, the incorporation of phylogenetics into introduction-based studies has placed the role of close relatives in facilitating or impeding invasion (Li et al. 2015, Park & Potter 2015) and the processes that are paramount when invasions occur (Takakura & Fujii 2015) into an evolutionary context. Introduced species also allow us to see over what timescales natives and invaders, now in novel sympatry, diverge, exhibit trait changes, or are outcompeted by exotic close

relatives and which forces (e.g., RI, enemies, mutualists, or resources) impose strongest selection on native species.

#### 5.4. Outlier Clades, Null Expectations, and Exceptions That Prove the Rule

Future studies will benefit from focusing on nontraditional clades for studying coexistence patterns. For example, we already know that we can find coexistence of close relatives in isolated habitats like islands, mountaintops, and isolated lakes. More studies of mainland taxa with high incidence of syntopic congeners at small spatial scales will provide useful information. An accumulation of such examples may allow us to understand the intrinsic and extrinsic factors enabling coexistence among close relatives. Conversely, species on islands that fail to radiate, when others do so, also provide ways to understand the conditions fostering coexistence in close relatives.

Identifying interesting outlier clades requires the development of null expectations of local coexistence. These nulls would allow us to ask questions such as, when do observed latitudinal species diversity gradients reflect an over- or underrepresentation of syntopic close relatives? Currently, studies generally generate null expectations of local coexistence on the basis of a stagnant, snapshot view of the contemporary regional species pool. However, more holistic eco-evolutionary nulls might illustrate at what scales—spatial or phylogenetic—patterns deviate from expectations. The development of null models of regional clade diversity (from simple random models with constant rates of speciation, extinction, and dispersal) could be extended to create null expectations for local coexistence of close relatives given regional processes.

### 6. CONCLUDING REMARKS

The study of coexistence in close relatives lies at the center of major paradoxes in biology. Close relatives provide useful models for how communities are built and assembled; yet truly understanding these dynamics will require integrative approaches incorporating biogeography, macroevolution, microevolution, behavior, and ecology.

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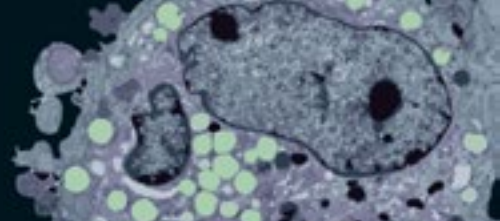
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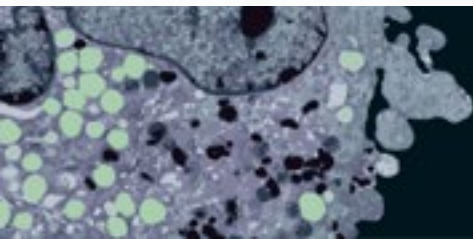
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