

Opinion

Evolutionary Community Ecology: Time to Think Outside the (Taxonomic) Box

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Ecologists and evolutionary biologists have long been interested in the role of interspecific competition in the diversification of clades. These studies often focus on a single taxonomic group, making the implicit assumption that important competitive interactions occur only between closely related taxa, despite abundant documentation of intense competition between species that are distantly related. Specifically, this assumption ignores convergence of distantly related competitors on limiting niche axes and thus may miss cryptic effects of distantly related competitors on the evolution of focal clades. For example, distantly related competitors may act as important drivers of niche conservatism within clades, a pattern commonly ascribed to evolutionary constraints or the abiotic environment. Here we propose an alternative model of how niche similarity evolves when the functional traits of interest are mediated by unrelated phenotypic traits, as is often the case for distantly related competitors. This model represents an important conceptual step towards a more accurate, taxonomically inclusive understanding of the role that competition plays in the micro- and macroevolution of interacting species.

A Taxonomically Constrained View Shaped by Sampling Limitations

There is growing recognition that both ecological and evolutionary processes shape contemporary **community** (see [Glossary](#)) patterns [1–3]. However, our understanding of evolutionary community ecology is limited by the tendency of studies to focus on species in a single taxonomic group, thus making the implicit assumption that relevant competitive interactions are limited to closely related taxa [4,5]. This assumption is at odds with a long history of empirical studies demonstrating that competition among distantly related species is ubiquitous in nature ([Table 1](#)), as well as with recent theoretical advances [6,7].

This taxonomically constrained bias emerges largely because, in many systems, sampling methods are taxon-group specific. For example, netting in ponds will capture fishes, but not birds. There may be important predatory and competitive interactions between these two groups ([Table 1](#)), but expanding the study scope to encompass both fishes and birds is both expensive and logistically challenging. Therefore, although data and theory show that we cannot assume a lack of competition between distantly related species based on phylogenetic and phenotypic divergence [6–8], quantifying competition directly is often precluded by the cost and difficulty of the required field observations and experimental manipulations.

Here we present justification for a shift to a more taxonomically inclusive approach to evolutionary community ecology and offer an emergent, conceptual model of the relationship between species relatedness, **functional trait** similarity, and competitive outcomes. This more taxonomically inclusive approach will be logistically and conceptually challenging, but

Highlights

Studies of evolutionary community ecology often assume that competitive interactions occur primarily and most intensely between closely related species, implicitly invoking the competition-relatedness hypothesis.

This competition-relatedness assumption is at odds with recent theory and a wealth of empirical studies demonstrating intense competition between distantly related species.

Here we provide an alternative, taxonomically inclusive framework for understanding the relationship between evolutionary relatedness and competitive interactions.

This framework indicates an approach to evolutionary community ecology that relies on field and experimental data to detect species interactions and resource overlap rather than inference from phylogenetic or morphological similarity alone.

A more accurate picture of the role that species interactions play in the assembly and evolution of communities will require that researchers think critically about their systems and be prepared to work outside traditional taxonomic constraints.

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Table 1. Examples of Competition between Distantly Related Animal Taxa^a

| Taxa | Competition type | Refs |
|-------------------------------------|-------------------|------------------------|
| Fish and ducks | Resource | [60–62] ^O |
| Salamanders and ducks | Resource | [63,64] ^O |
| Insects and fish | Resource | [65] ^O |
| Birds, squirrels, and primates | Resource | [66,67] ^O |
| Salamanders, insects, and arachnids | Interference | [68–70] ^{O/E} |
| Amphibian larvae and insects | Resource | [71,72] ^E |
| Mammals, snails, and insects | Resource | [73,74] ^E |
| Plants, arachnids, and toads | Resource | [75,76] ^{O/E} |
| Plants and fish | Resource | [77] ^E |
| Rodents and insects | Resource | [21,78] ^{O/E} |
| Mammals and birds | Interference | [79–81] ^{O/E} |
| Insects and birds | Interference | [82,83] ^O |
| Fish and amphibians | Interference | [84] ^E |
| Ungulates and hares | Resource/Apparent | [85,86] ^O |
| Canine and feline predators | Resource | [87] ^O |
| Crabs and gastropods | Resource | [88] ^{O/E} |
| Insects and birds | Resource | [89] |

^aCompetition between distantly related taxa has been found across marine, terrestrial, and freshwater systems. Columns show the taxa involved in competition, competition type (resource or **interference**; in one example '**apparent competition**' may also have contributed to observed patterns), and citations (observational and experimental studies indicated with O and E superscripts following references). Ecological and evolutionary studies may miss important species interactions if they fail to consider potential competitors of intermediate and deep evolutionary divergence.

we cannot ignore the fact that ecological and evolutionary research focusing only on within-clade interactions is both unrepresentative of natural systems and potentially misleading. Distantly related competitors may act as selective pressures that regulate the diversification of entire clades [9–11]. Consequently, effects of competition with divergent taxa on the phylogenetic structure of a focal clade may be misinterpreted as originating from constraints and interactions within that clade.

Beyond logistical challenges, this taxonomically inclusive perspective poses conceptual obstacles, including how to generate predictions that do not hinge only on the similarity of homologous, **phenotypic traits** but also incorporate convergent evolution of resource use [6,8–10]. More fundamentally, this approach will require researchers to think outside the boundaries of their own taxonomic expertise and experience. Traditional distinctions such as 'plant ecology', 'animal ecology', and 'fish ecology' may poorly serve our understanding of larger community processes and hamper communication of theoretical advances across systems. We hope this paper spurs the field of evolutionary community ecology forward, beyond the conceptual and empirical constraints of the taxonomically constrained view and towards research that reflects the true diversity of species interactions shaping ecological communities.

An Implicit Model of Evolutionary Community Ecology

The implicit assumption of taxonomically constrained studies is that competitive interactions are limited to closely related taxa, requiring: (i) that **niche similarity** is a function of phenotypic trait similarity, which declines with evolutionary divergence; and (ii) that the selective strength of

Glossary

Apparent competition: where competition is mediated through a shared predator.

Asymmetric competitive interactions: where the *per capita* competitive effect of species A on species B is greater than that of species B on species A. The extreme case is amensalism, where only one taxon is affected by the competitive interaction.

Character displacement: the adaptive divergence of traits due to competition between sympatric taxa.

Clade: all descendant taxa of a single ancestor. Thus, members of the same clade are more closely related to each other than to all taxa outside the clade.

Coexistence: where multiple taxa reliant on a shared resource persist in sympatry due to stabilizing mechanisms.

Community: the local set of co-occurring and potentially interacting individuals of all taxa.

Competition-relatedness hypothesis: the hypothesis that competition is strongest between more closely related taxa and declines with phylogenetic divergence.

Competitive ability similarity: how similar two taxa are in their ability to compete for a shared resource.

Competitive exclusion: where co-occurrence of taxa is prevented because a taxon has been locally extirpated by competition.

Diffuse competition: competition with two or more other taxa.

Functional redundancy: that multiple taxa in a community share the same ecological role.

Functional trait: the ecological role or action of a characteristic of an organism.

Interference competition: where competition is mediated through direct interactions between individuals, such as aggression.

Limiting similarity: hypothesis that there is some maximum level of niche similarity for which coexistence of taxa is possible.

Metabarcoding: massively parallel sequencing of PCR-enriched taxonomically informative regions of the genome to infer the composition of multitaxon assemblages.

competition increases with phenotypic trait similarity (i.e., the **limiting similarity** hypothesis; [Box 1](#)). These assumptions can be traced to Darwin's [11] **competition-relatedness hypothesis**, which predicts that interspecific competition is most intense between closely related taxa. This hypothesis is often invoked explicitly in studies inferring ecological processes from community phylogenetic patterns [4,12,13].

The limiting similarity hypothesis posits that **competitive exclusion** occurs when the niche space of taxa overlap [14,15]. This, in turn, yields the prediction that competition between closely related taxa (assumed to have the greatest niche overlap due to shared phenotypic traits) will lead to **phylogenetic over-dispersion** in ecological communities or, alternatively, to the evolution of trait and niche differences between closely related taxa to facilitate **coexistence** [16,17]. The competition-relatedness hypothesis is also implicit in the concept of '**functional redundancy**', which assumes that closely related species of similar morphology have essentially the same functional traits and – by the same logic – that distantly related species have different functional traits [9].

Niche conservatism: the tendency for traits that determine a taxon's ecological niche to be more similar among closely related taxa than expected by phylogenetic distance.

Niche similarity: the extent of overlap in the resource needs of different taxa.

Phenotypic trait: a physical or behavioral characteristic of an organism.

Phylogenetic over-dispersion: where taxa in a community are more distantly related than expected by chance.

Box 1. Competition and Niche Convergence

Niche similarity is a central driver of competitive interactions. Historically, limiting similarity – the hypothesis that some minimum level of niche difference between taxa is necessary for coexistence because competition intensity increases with niche similarity [90] – has played an important role in how we understand evolutionary community ecology. The hypothesis predicts that competition will drive exclusion or character displacement when multiple taxa compete for the same niche space. Although recent developments in coexistence theory have provided a more nuanced perspective where competitive outcomes are also mediated by competitive ability similarity [7,18], niche overlap is the fundamental determinant of whether there is any competitive interaction between taxa. Thus, prediction and measurement of niche similarity is of great interest in evolutionary community ecology.

The competition-relatedness hypothesis predicts niche space overlap based on phylogenetic relatedness. Often, trait-based approaches seek to identify key phenotypic traits underlying the niche, which can then be compared across taxa. However, the overall extent of niche space overlap is not necessarily relevant to the intensity of competition between taxa. In some cases convergence on a single limiting niche axis will mediate competition (e.g., a shared food resource), even if there is little or no overlap along other niche axes ([Figure I](#)). As a result, it is critical to identify limiting niche axes – which may or may not be phylogenetically conserved – relevant to competitive exclusion and character displacement. Here, we call for a renewed focus on these shared resources as the truly relevant functional trait because niche overlap cannot be predicted from phylogenetic distance or from homologous phenotypic traits for distantly related taxa.

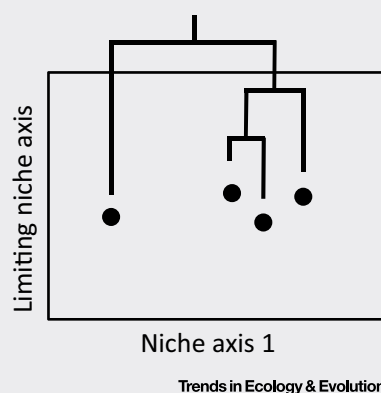


Figure I. Convergence of Distantly Related Taxa along Limiting Niche Axes. Competition occurs only for limiting factors, which may represent a small proportion of total niche space. Distantly related taxa need only converge along these critical, limiting niche axes to compete. In this example, niche axis 1 (x-axis) is phylogenetically conserved (only closely related taxa have similar niches). However, there is convergence between members of the focal clade and the distantly related outgroup along the limiting niche axis (y-axis).

The extent to which taxonomically biased sampling constrains studies of evolutionary community ecology is not uniform across systems. For example, sampling approaches for plants have low taxonomic bias. As a result, studies of plant communities generally cover a broader taxonomic scope than studies of animal communities (e.g. [6]), and the argument for a taxonomically inclusive perspective may be intuitive to plant ecologists. Nevertheless, 'plant' ecology carries its own taxonomic bias, and interactions with both animals and microbes have important consequences for plant assemblages (Table 1). We hope, therefore, that our taxonomically inclusive conceptual model will be applicable and useful across plant- and animal-dominated study systems.

Competition Is Often Unrelated to Phylogeny or Phenotypic Trait Values

There are several problems with the competition-relatedness hypothesis. First, recent theoretical developments reveal that coexistence is shaped not only by niche similarities but also by competitive ability similarities [18]. Thus, phylogenetic over-dispersion is only one possible outcome of competition mediated by traits with a phylogenetic pattern [7,10]. These theoretical predictions are consistent with mixed empirical support for the competition-relatedness hypothesis [6,19,20]. Secondly, phylogenetic distance is a poor predictor of functional trait similarity at deep levels of divergence. For phenotypic traits, Letten and Cornwell [8] found that: (i) we expect trait similarity to decline nonlinearly with evolutionary divergence; and (ii) variance increases with divergence due to convergent evolution of trait values. Similarly, Godoy *et al.* [6] found no significant relationship between niche similarity and phylogenetic distance in grassland plants. More fundamentally (and our focus here), competition need not be mediated by shared phenotypic traits at all but may also emerge due to convergent evolution of distantly related taxa [9,10]. These findings call into question the central assumptions of taxonomically constrained approaches to community evolution, but – perhaps more importantly – they also demand a closer consideration of the relationship between species traits and competitive interactions.

A well-studied example of competition between desert rodent and ant seed predators underscores the challenge of evolutionary community ecology when phenotypic trait overlap does not reflect the strength of competition [21]. In describing this system, Reichman [22] observes:

'Using the traditional approach to investigations of competition, one might ask in what ways are ants and rodents different. The answer, of course, is that they are different in almost every way except that they use the same food.'

Here, there are likely to be no common, phenotypic traits underlying competition that could be used to infer species interactions or their role in shaping communities. That is, the shared functional trait (seed predator) is mediated by unrelated phenotypic traits. This lack of phenotypic trait overlap in no way reflects a lack of ecological and evolutionary importance of rodent–ant interactions in desert communities. Instead, the importance of these interactions is best predicted by shared reliance on a limited resource – seeds – that can be exploited via a range of different strategies each with its own set of key phenotypic traits. Further, although the evolution of phenotypic traits for seed exploitation by both ants and rodents is certainly shaped by evolutionary constraints within each of the lineages (i.e., the range of possible trait values within ants), those constraints are different for each lineage.

This observation by Reichman [22] and others (Table 1) show that taxa need not be phenotypically similar to have strong competitive interactions, allowing a much looser relationship between phenotypic traits and the strength of competition than is predicted by the competition-relatedness hypothesis, which is implicitly assumed in studies that focus on phenotypic

traits (Box 1). Levin [23] showed that only interactions for limiting resources determine the intensity of competition, such that ‘certain dimensions of the [niche] hypervolumes are of paramount importance’. The key implication of Levin’s classic work is that convergence on just one or a few resources is needed to produce strong competition between divergent taxa.

In addition to being unpredictable based on phylogenetic relatedness, competition between distantly related taxa tends to be more **asymmetric** than competition between closely related taxa [6,24]. As lineages diverge not only does their niche similarity but also their relative competitive ability, such that coexistence of some distantly related species pairs may be less likely than coexistence of closely related species with similar competitive abilities [7,25,26]. For example, in a test of the competition-relatedness hypothesis Barnes [27] found that competition for space was greater between distantly related bryozoans and ascidians (interfamily to interkingdom) than between closely related taxa (congenerics).

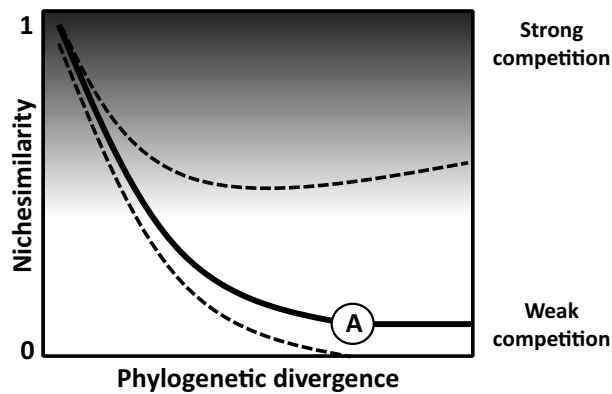
These competitive interactions between distantly related species – and the resulting evolutionary implications within local communities – are entirely missing from taxonomically constrained studies of community evolution, where analyses address only variation within focal lineages. More broadly, strong competitive interactions between distantly related species underscore a fundamental constraint of approaches that rely on phenotypic trait overlap as an index of the strength of competition, in both ecological and evolutionary contexts. These phenotypic traits are only shared, and only have phylogenetic patterns, within lineages of closely related taxa. Thus, this approach removes from consideration the innumerable natural communities that encompass strong interaction between distantly related taxa that lack phenotypic trait overlap.

An Alternative Model of Competition and Phylogenetic Divergence

To address the limitations of the taxonomically constrained view, we propose an alternative model of the relationship between phylogenetic divergence, phenotypic and functional trait similarity, and competition that covers a wider range of taxonomic relatedness (Figure 1). As described in models of the distribution of competitive abilities and functional similarity across phylogenetic distance [6,9], our model assumes that closely related taxa will tend to have high niche and **competitive ability similarity** due to high trait overlap (both phenotypic and functional). By contrast, divergent taxa will have very low phenotypic trait overlap, resulting in low niche overlap on average. However, distantly related taxa can evolve convergent reliance on a shared resource and so have high niche overlap due to shared functional traits. These shared functional traits, because they are not constrained by a shared phenotypic basis or evolutionary history, will tend to result in large differences in competitive ability [7,28,29]. Importantly, our taxonomically inclusive model also predicts that mean niche similarity declines with phylogenetic divergence but variation in niche similarity increases with phylogenetic divergence [8,30]. This conceptual model reconciles the seemingly contradictory observations that: (i) there is sometimes a phylogenetic pattern in phenotypic traits mediating competition within clades; (ii) most distantly related taxa are not competitors; and yet (iii) distantly related taxa can be intense competitors. An emergent prediction of this model is that there will be rare resource convergence in distantly related taxa that can exert strong effects on trait overlap and phylogenetic concurrence patterns (e.g., over-dispersion, clustering) within clades of closely related focal taxa.

Clade-Level Effects of Competition between Distantly Related Taxa

We know that all forms of species interaction can act as strong selective forces. Examples include coevolution of mutualists and predator–prey and pathogen–host pairs [31]. However,



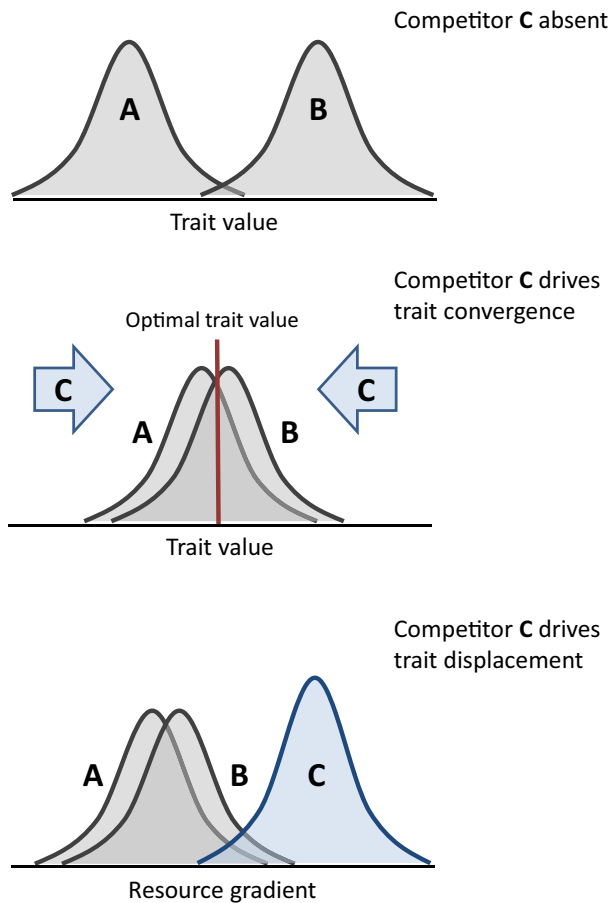
Trends in Ecology & Evolution

Figure 1. A Model of How Niche Similarity Evolves at Deep Levels of Divergence. As supported by empirical studies and theory, mean niche similarity of taxa (0 = no similarity, 1 = identical niche) declines with phylogenetic distance, but this decline is asymptotic because traits underlying niche similarity can converge over time (unbroken line). Simultaneously, the variance in niche similarity increases (broken lines), as does the mean difference in competitive ability (not shown). We argue that, at some deep level of divergence (point A in the figure), taxa no longer compete for resources using shared phenotypic traits. At this point most taxa share essentially no limiting resource axes so mean niche similarity is almost zero. However, the mean is not zero because distantly related taxa can converge on shared functional traits that are mediated by distinct phenotypic traits. Because these phenotypic traits share no common ancestor, the degree of niche similarity is unrelated to phylogenetic distance (the slope after point A is ≈ 0). As a result, the strength of competition (shading) is not necessarily related to phylogenetic distance or phenotypic trait similarity.

the evolutionary response to competition – ecological **character displacement** – has long been viewed as a key process shaping the diversity of species [17,32,33]. Studies of character displacement have focused on closely related taxa [17], but competition between divergent taxa may also shape patterns of character displacement within clades of closely related species. For example, competition with other finches and with carpenter bees may have influenced the evolution of resource use and body size of some Galápagos finch species [34].

We predict that competition with distantly related taxa may affect niche and trait (both phenotypic and functional) diversification within clades through at least two nonexclusive mechanisms (Figure 2). First, distantly related competitors may exert a selective pressure that promotes trait convergence in members of a focal clade. Specifically, closely related taxa may evolve similar traits that allow persistence in the presence of a shared, distantly related competitor (a special case of convergent evolution). This process requires strong competition with the distantly related taxon, such that selection for traits that reduce competition with the distantly related taxon overwhelms selection for trait divergence to reduce competition among members of the focal clade. This effect may be further facilitated by **diffuse competition** among closely related taxa that reduces their relative fitness [35].

A strong competitive effect is most likely to occur when competitive interactions between distantly related taxa are highly asymmetric [6,24]. For example, freshwater streams and ponds are often home to co-occurring and closely related species of amphibians and invertebrates that experience strong competition and predation from fish [36,37]. In these systems trait convergence among closely related members of amphibian and invertebrate clades may, in part, be a result of the strong selective pressure imposed by distantly related fish [38,39]. Such trait convergence also creates neutral community dynamics within clades, where ecological equivalence can promote long-term sympatry [40,41].



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Figure 2. Potential Influence of Distantly Related Competitors on Diversification within a Focal Clade. When distantly related competitors are absent, we expect trait and niche diversification within clades of sympatric taxa due to character displacement (top). However, distantly related competitors may act as selective pressures that reduce trait divergence (and diversification) within focal clades by creating a shared optimal trait value for multiple members of the focal clade (middle) or by directional character displacement on members of the focal clade (bottom).

Second, competition with distantly related taxa may act as a directional selective pressure constraining evolution within a focal clade. This mechanism is inherent to the concept of ecological or competitive release, where the absence of competitors results in ecological opportunity allowing adaptive radiation within a clade [17,42,43]. Well-studied adaptive radiations that have been attributed to character displacement, including Galápagos finches and postglacial lake three-spine sticklebacks, are characterized by colonization of novel habitats with few or no other competitors [17,44–46]. In these systems divergence of traits within the focal clade is thought to be promoted by the absence of other competitors. However, the same logic predicts that the presence of other, distantly related competitors will constrain the degree of trait divergence within a focal clade. For example, Pires *et al.* [47] observed that competition between clades of mammal carnivores reduced the influence of within-clade competition on diversification, demonstrating the potential for an important effect of distantly related competitors on within-clade evolutionary dynamics.

An Ecological Mechanism for Niche Conservatism

In general, we predict that the influence of a distantly related competitor will tend to result in less trait and niche divergence within a clade when that competitor is present than when it is absent. That is, the distantly related competitor may act as a selective pressure causing **niche conservatism** within the focal clade [48,49]. In failing to consider the effects of the distantly related competitor, these patterns of within-clade divergence could be misinterpreted as being driven by other mechanisms, such as evolutionary constraints and selection from the abiotic environment. However, they would in fact reflect a reduced role of within-clade competition due to strong competition with the distantly related taxon. We propose that competition with distantly related taxa may be an important ecological mechanism limiting trait and niche diversification and shaping observed patterns of niche conservatism.

One way to detect niche conservatism shaped by competition with distantly related taxa would be to compare the strength of competition between members of the focal clade and the putative distantly related competitor. Strong asymmetry, where the distantly related competitor has a larger competitive influence on one or more members of the focal clade than members of the focal clade have on each other, would suggest that competition with the distantly related taxa exerts a stronger selective force than other taxa of the same clade. A lack of trait and niche divergence within the focal clade may be a function of limited ecological opportunity imposed by the distantly related competitor. Where studies have compared the strength of competition between closely and distantly related taxa, distantly related taxa are often found to have larger competitive effects. For example, Reseterits [50] found that, contrary to the limiting similarity hypothesis, competition from a distantly related, morphologically divergent, and smaller fantail darter had a stronger influence on mottled sculpin condition and growth than the larger and closely related Kanawha sculpin.

Stronger evidence for this process of ecologically driven niche conservatism would require comparison of communities with and without the putative distantly related competitor. Under apparent niche conservatism, we predict that phylogenetic clustering within the focal clade (i.e., the occurrence of individual species) or the degree of trait overlap among members of the focal clade will be greater in the presence (and/or varying with abundance) of the distantly related competitor. Perhaps the best example of this comes from three-spine sticklebacks. Schluter *et al.* [17] describe the likely role that sculpins play in constraining the evolution of three-spine sticklebacks in postglacial lakes. Pairs of stickleback species, which are thought to be the product of character displacement following double invasion by a single founding species, are found only in lakes without competing/intraguild predator sculpin. Further, sticklebacks that co-occur with sculpin are ecologically and morphologically different from sticklebacks in lakes without sculpin, suggesting that competition with sculpin also drives directional character displacement [44,51,52].

Currently, guilds of putative competitors are often assembled based only on relatedness, which may miss these potentially important interactions [5]. Identification of putative distantly related competitors and understanding their role in clade diversification will require a move beyond phylogenies and measures of phenotypic trait similarity to infer competition. More intensive field studies will be necessary to isolate limiting niche axes and to identify the taxa that use them – regardless of phylogenetic relatedness. New molecular tools have made these field studies more feasible than ever before. High-throughput sequencing is increasingly used to detect a wide range of taxa (i.e., **metabarcoding** to detect taxa from noninvasive samples) [53]. These tools tend to be less taxonomically biased than traditional sampling approaches, providing a more inclusive view of community membership [54]. Improved data on species presence alone

provide novel insight on species interactions through the analysis of correlation networks, which can be used to identify potentially interacting taxon pairs [55–57]. Molecular diet analysis has also been used to reveal previously unknown patterns of resource overlap and partitioning (e.g. [58]). For example, Brown *et al.* [59] used molecular diet analysis to reveal resource overlap and putative competition between Telfair's skink and Asian musk shrew – distantly related species for which the extent of niche overlap would be unpredictable from phenotypic traits or phylogenetic relatedness. The increasing use of molecular tools in ecological research will continue to expand our understanding of the frequency and strength of species interactions across taxonomic boundaries (see Outstanding Questions).

Concluding Remarks

Theory and empirical data predict important competitive interactions between divergent taxa but most studies of evolutionary community ecology are taxonomically constrained, considering competition only among closely related members of a focal clade. Critically, this narrow taxonomic view may miss cryptic effects of competitive interactions among distantly related taxa that influence patterns of diversification within the focal clade. Competition between distantly related taxa is frequently documented in field studies, suggesting that it has played an important role in the evolution of biodiversity on a global scale. Our understanding of the maintenance of that biodiversity, and of species diversification in general, will be substantially advanced by explicitly addressing competition between distantly related taxa in studies of evolutionary community ecology.

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References

- Schoener, T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331, 426–429
- Weber, M.G. *et al.* (2017) Evolution in a community context: on integrating ecological interactions and macroevolution. *Trends Ecol. Evol.* 32, 291–304
- Mittelbach, G.G. and Schemske, D.W. (2015) Ecological and evolutionary perspectives on community assembly. *Trends Ecol. Evol.* 30, 241–247
- Clarke, M. *et al.* (2017) Trait evolution in adaptive radiations: modelling and measuring interspecific competition on phylogenies. *Am. Nat.* 189, 121–137
- Simberloff, D. and Dayan, T. (1991) The guild concept and the structure of ecological communities. *Annu. Rev. Ecol. Syst.* 22, 115–143
- Godoy, O. *et al.* (2014) Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.* 17, 836–844
- Mayfield, M.M. and Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* 13, 1085–1093
- Letten, A.D. and Cornwell, W.K. (2015) Trees, branches and (square) roots: why evolutionary relatedness is not linearly related to functional distance. *Methods Ecol. Evol.* 6, 439–444
- Reseratis, W.J. and Chalcraft, D.R. (2007) Functional diversity within a morphologically conservative genus of predators: implications for functional equivalence and redundancy in ecological communities. *Funct. Ecol.* 21, 793–804
- Gerhold, P. *et al.* (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Funct. Ecol.* 29, 600–614
- Darwin, C.R. and Wallace, A.R. (1858) On the tendency of species to form varieties and on the perpetuation of varieties and species by natural means of selection. *Zool. J. Linn. Soc.* 3, 46–50
- Narwani, A. *et al.* (2015) Using phylogenetics in community assembly and ecosystem functioning research. *Funct. Ecol.* 29, 589–591
- Vamosi, S.M. *et al.* (2008) Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol. Ecol.* 18, 572–592
- MacArthur, R. and Levins, R. (1976) The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101, 377–385
- Gause, G.F. (1934) *The Struggle for Existence*, Williams & Wilkins
- Violle, C. *et al.* (2011) Phylogenetic limiting similarity and competitive exclusion. *Ecol. Lett.* 14, 782–787
- Schluter, D. (2000) Ecological character displacement in adaptive radiation. *Am. Nat.* 156, S4–S16
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366
- Cahill, J.F. *et al.* (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspect. Plant Ecol. Evol. Syst.* 10, 41–50
- Alexandrou, M.A. *et al.* (2014) Evolutionary relatedness does not predict competition and co-occurrence in natural or experimental communities of green algae. *Proc. Biol. Sci.* 282, 20141745
- Brown, J. and Davidson, D. (1977) Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196, 880–882

Outstanding Questions

Are there emergent characteristics of communities that predict the relative frequency of competition between distantly related taxa (e.g., resource availability, species diversity, productivity, mean and variance of interaction strengths)?

Are there clade characteristics associated with a greater role of competition between clade members versus distantly related taxa (e.g., branch length, species number, niche conservatism)?

Are certain types of competition (e.g., exploitative, interference) more likely than others to occur between distantly related taxa?

At what evolutionary depth does niche space become divorced from phenotypic trait value? Does this evolutionary depth vary by taxonomic group (e.g., plants versus animals) or by functional traits (e.g., herbivores versus carnivores)?

How does the presence of diffuse competition change the potential effects of distantly related competitors on focal clade diversification? Is diffuse competition more relevant to closely or distantly related competitors?

How commonly is 'niche conservatism' driven by competition with distantly related taxa?

22. Reichman, O. (1979) Introduction to the symposium: competition between distantly related taxa. *Am. Zool.* 19, 150–151
23. Levin, S.A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat.* 104, 413–423
24. Levins, R. (1979) Asymmetric competition among distant taxa. *Am. Zool.* 19, 1097–1104
25. Germain, R.M. *et al.* (2016) Species coexistence: macroevolutionary relationships and the contingency of historical interactions. *Proc. Biol. Sci.* 283, 20160047
26. Weber, M.G. and Strauss, S.Y. (2016) Coexistence in close relatives: beyond competition and reproductive isolation in sister taxa. *Annu. Rev. Ecol. Evol. Syst.* 47, 359–381
27. Barnes, D.K. (2003) Competition asymmetry with taxon divergence. *Proc. Biol. Sci.* 270, 557–562
28. Shtilerman, E. *et al.* (2015) Emergence of structured communities through evolutionary dynamics. *J. Theor. Biol.* 383, 138–144
29. Hillerislambers, J. *et al.* (2012) Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.* 43, 227–248
30. Kelly, S. *et al.* (2014) Phylogenetic trees do not reliably predict feature diversity. *Divers. Distrib.* 20, 600–612
31. Hendry, A. (2016) *Eco-evolutionary Dynamics*, Princeton University Press
32. Brown, W. and Wilson, E. (1956) Character displacement. *Syst. Zool.* 5, 49–64
33. Dayan, T. and Simberloff, D. (2005) Ecological and community-wide character displacement: the next generation. *Ecol. Lett.* 8, 875–894
34. Schluter, D. (1986) Character displacement between distantly related taxa? Finches and bees in the Galápagos. *Am. Nat.* 127, 95–102
35. Stump, S.M. (2017) Multispecies coexistence without diffuse competition; or, why phylogenetic signal and trait clustering weaken coexistence. *Am. Nat.* 190, 213–228
36. McPeck, M.A. (1990) Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* 71, 83–98
37. Wellborn, G. *et al.* (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.* 27, 337–363
38. Richardson, J.M.L. (2001) The relative roles of adaptation and phylogeny in determination of larval traits in diversifying anuran lineages. *Am. Nat.* 157, 282–299
39. Strobbe, F. *et al.* (2011) Fish predation selects for reduced foraging activity. *Behav. Ecol. Sociobiol.* 65, 241–247
40. Siepielski, A.M. *et al.* (2010) Experimental evidence for neutral community dynamics governing an insect assemblage. *Ecology* 91, 847–857
41. Holt, R.D. (2006) Emergent neutrality. *Trends Ecol. Evol.* 21, 531–533
42. Simpson, G. (1953) *The Major Features of Evolution*, Columbia University Press
43. Stroud, J.T. and Losos, J.B. (2016) Ecological opportunity and adaptive radiation. *Annu. Rev. Ecol. Evol. Syst.* 47, 507–532
44. Schluter, D. (2016) Speciation, ecological opportunity, and latitude. *Am. Nat.* 187, 1–18
45. Grant, P. and Grant, B. (2006) Evolution of character displacement in Darwin's finches. *Science* 313, 224–226
46. Schluter, D. and McPhail, J.D. (1992) Ecological character displacement and speciation in sticklebacks. *Am. Nat.* 140, 85–108
47. Pires, M.M. *et al.* (2017) Interactions within and between clades shaped the diversification of terrestrial carnivores. *Evolution* 71, 1855–1864
48. Wiens, J.J. *et al.* (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* 13, 1310–1324
49. Crisp, M.D. and Cook, L.G. (2012) Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes? *New Phytol.* 196, 681–694
50. Reseratis, W. (1995) Limiting similarity and the intensity of competitive effects on the mottled sculpin, *Cottus bairdi*, in experimental stream communities. *Oecologia* 103, 31–38
51. Miller, S.E. *et al.* (2015) Intraguild predation leads to genetically based character shifts in the threespine stickleback. *Evolution* 69, 3194–3203
52. Bolnick, D.I. *et al.* (2003) The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161, 1–28
53. Creer, S. *et al.* (2016) The ecologist's field guide to sequence-based identification of biodiversity. *Methods Ecol. Evol.* 56, 68–74
54. Leray, M. and Knowlton, N. (2016) Censusing marine eukaryotic diversity in the twenty-first century. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 371, 20150331
55. Vacher, C. *et al.* (2016) Learning ecological networks from next-generation sequencing data. *Adv. Ecol. Res.* 54, 1–39
56. Evans, D.M. *et al.* (2016) Merging DNA metabarcoding and ecological network analysis to understand and build resilient terrestrial ecosystems. *Funct. Ecol.* 30, 1904–1916
57. Bohan, D.A. *et al.* (2017) Next-generation global biomonitoring: large-scale, automated reconstruction of ecological networks. *Trends Ecol. Evol.* 32, 477–487
58. Kartzinel, T.R. *et al.* (2015) DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proc. Natl. Acad. Sci. U. S. A.* 112, 8019–8024
59. Brown, D.S. *et al.* (2014) Dietary competition between the alien Asian musk shrew (*Suncus murinus*) and a re-introduced population of Telfair's skink (*Leiolopisma telfairi*). *Mol. Ecol.* 23, 3695–3705
60. Väänänen, V.M. *et al.* (2012) Fish–duck interactions in boreal lakes in Finland as reflected by abundance correlations. *Hydrobiologia* 697, 85–93
61. Hunter, M.L. *et al.* (1986) Duckling responses to lake acidification: do black ducks and fish compete? *Okios* 47, 26–32
62. Eriksson, M. (1979) Competition between freshwater fish and goldeneyes *Bucephala clangula* (L.) for common prey. *Oecologia* 41, 99–107
63. Benoy, G.A. *et al.* (2002) Patterns of habitat and invertebrate diet overlap between tiger salamanders and ducks in prairie potholes. *Hydrobiologia* 481, 47–59
64. Benoy, G.A. (2005) Variation in tiger salamander density within prairie potholes affects aquatic bird foraging behaviour. *Can. J. Zool.* 83, 926–934
65. Englund, G. *et al.* (1992) Asymmetric competition between distant taxa: poeciliid fishes and water striders. *Oecologia* 92, 498–502
66. Beaudrot, L. *et al.* (2013) Interspecific interactions between primates, birds, bats, and squirrels may affect community composition on Borneo. *Am. J. Primatol.* 75, 170–185
67. Beaudrot, L. *et al.* (2013) Co-occurrence patterns of Bornean vertebrates suggest competitive exclusion is strongest among distantly related species. *Oecologia* 173, 1053–1062
68. Hickerson, C.A.M. *et al.* (2004) Behavioral interactions between salamanders and centipedes: competition in divergent taxa. *Behav. Ecol.* 15, 679–685
69. Hickerson, C.-A.M. *et al.* (2012) Interactions among forest-floor guild members in structurally simple microhabitats. *Am. Midl. Nat.* 168, 30–42
70. Gall, S.B. *et al.* (2003) Do behavioral interactions between salamanders and beetles indicate a guild relationship? *Am. Midl. Nat.* 149, 363–374
71. Mokany, A. and Shine, R. (2003) Competition between tadpoles and mosquito larvae. *Oecologia* 135, 615–620
72. Morin, P. *et al.* (1988) Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. *Ecology* 69, 1401–1409

73. Huntzinger, M. *et al.* (2011) Small mammals cause non-trophic effects on habitat and associated snails in a native system. *Oecologia* 167, 1085–1091
74. Huntzinger, M. *et al.* (2008) Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology* 89, 1972–1980
75. Jennings, D.E. *et al.* (2010) Evidence for competition between carnivorous plants and spiders. *Proc. Biol. Sci.* 277, 3001–3008
76. Jennings, D.E. *et al.* (2016) Foraging modality and plasticity in foraging traits determine the strength of competitive interactions among carnivorous plants, spiders and toads. *J. Anim. Ecol.* 85, 973–981
77. Davenport, J.M. and Riley, A.W. (2017) Complex inter-kingdom interactions: carnivorous plants affect growth of an aquatic vertebrate. *J. Anim. Ecol.* 86, 484–489
78. Brown, J. *et al.* (1979) An experimental study of competition between seed-eating desert rodents and ants. *Am. Zool.* 19, 1129–1143
79. Kobayashi, F. *et al.* (2014) Potential resource competition between an invasive mammal and native birds: overlap in tree cavity preferences of feral raccoons and Ural owls. *Biol. Invasions* 16, 1453–1464
80. Lambrechts, M.M. *et al.* (2007) Cavity-nesting black rats in distinct Corsican oak habitats and their potential impact on breeding Paridae. *Folia Zool.* 56, 445–448
81. Sarà, M. *et al.* (2005) Exploitation competition between hole-nesters (*Muscardinus avellanarius*, Mammalia and *Parus caeruleus*, Aves) in Mediterranean woodlands. *J. Zool.* 265, 347–357
82. Veiga, J.P. *et al.* (2013) Interaction between distant taxa in the use of tree cavities in African ecosystems: a study using nest-boxes. *J. Trop. Ecol.* 29, 187–197
83. Efstathion, C.A. *et al.* (2015) A push–pull integrated pest management scheme for preventing use of parrot nest boxes by invasive Africanized honey bees. *J. Field Ornithol.* 86, 65–72
84. Resetarits, W.J. (1995) Competitive asymmetry and coexistence in size-structured populations of brook trout and spring salamanders. *Oikos* 73, 188–198
85. Belovsky, G.E. and Arbor, A. (1984) Moose and snowshoe hare competition and a mechanistic explanation from foraging theory. *Oecologia* 61, 150–159
86. Arthur, S. and Prugh, L. (2010) Predator mediated indirect effects of snowshoe hares on Dall's sheep in Alaska. *J. Wildl. Manage.* 74, 1709–1721
87. Elbroch, L.M. *et al.* (2015) Recolonizing wolves influence the realized niche of resident cougars. *Zool. Stud.* 54, 1–11
88. Morton, B. and Yuen, W.Y. (2000) The feeding behaviour and competition for carrion between two sympatric scavengers on a sandy shore in Hong Kong: the gastropod, *Nassarius festivus* (Powys) and the hermit crab, *Diogenes edwardsii* (De Haan). *J. Exp. Mar. Biol. Ecol.* 246, 1–29
89. Haemig, P. (1996) Interference from ants alters foraging ecology of great tits. *Behav. Ecol. Sociobiol.* 38, 25–29
90. Abrams, P. (1983) The theory of limiting similarity. *Annu. Rev. Ecol. Syst.* 14, 359–376