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## COEXISTENCE OF THE NICHE AND NEUTRAL PERSPECTIVES IN COMMUNITY ECOLOGY

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**Abstract.** The neutral theory for community structure and biodiversity is dependent on the assumption that species are equivalent to each other in all important ecological respects. We explore what this concept of equivalence means in ecological communities, how such species may arise evolutionarily, and how the possibility of ecological equivalents relates to previous ideas about niche differentiation. We also show that the co-occurrence of ecologically similar or equivalent species is not incompatible with niche theory as has been supposed, because niche relations can sometimes favor coexistence of similar species. We argue that both evolutionary and ecological processes operate to promote the introduction and to sustain the persistence of ecologically similar and in many cases nearly equivalent species embedded in highly structured food webs. Future work should focus on synthesizing niche and neutral perspectives rather than dichotomously debating whether neutral or niche models provide better explanations for community structure and biodiversity.

**Key words:** coexistence; ecological similarity; equivalence; neutral theory; niche differentiation; speciation.

### INTRODUCTION

The role of niche differentiation has long been invoked as essential in maintaining biodiversity at different scales. Such niche differentiation involves a very large number of possible factors including resources, enemies, mutualists, habitats, temporal and spatial patchiness, as well as distinct responses to conspecifics via either direct (e.g., territoriality, mating competition) or indirect (and often unspecified) mechanisms (see Chesson 2000, Chase and Leibold 2003). This broad array of mechanisms has, however, been recently contrasted with a “neutral” perspective in which none of these mechanisms operate, because species do not differ from one another in any ways that distinguish their population dynamics (Bell 2001, Hubbell 2001; see Chave 2004 for a historical review). The significance and magnitude of these neutral processes in shaping biodiversity patterns is unclear in comparison to processes involving niche differentiation—the equalizing and stabilizing effects, respectively, described by Chesson (2000). The relative roles of niche and neutral processes in structuring biodiversity will depend on how likely and how frequently ecologically equivalent species are created by speciation processes, how species adapt to one another and to their common environments, and the particulars of how they enter and interact in communities and metacommunities if they do evolve.

We come to this problem from two very different paths. One of us works on taxa in which different genotypes in the same population often show greater levels of niche differentiation than are apparent among many species (Leibold and Tessier 1991, Leibold et al. 1994, Tessier and Leibold 1997). The other works on taxa having many locally co-occurring species that are frequently difficult if not impossible to identify as separate species for much of their life cycle, let alone discriminate their ecological distinctions (McPeck 1998, 2004, McPeck and Wellborn 1998, McPeck and Brown 2000; Turgeon et al. 2005). Thus, our perspectives are shaped by experiences with taxa that probably span the gamut of possibilities for niche and neutral perspectives, even though we both have studied how all these various taxa live and interact with one another in some of the same ponds and lakes across North America.

No doubt can exist about the general importance of niche differentiation in shaping the dynamics of interacting species and in regulating how species coexist at different scales (Tilman and Pacala 1993, Chesson 2000, Chase and Leibold 2003). We think it is ludicrous to imagine entire ecosystems of hundreds of interacting species that would show no niche differentiation and thus be governed by purely neutral dynamics. However, we see three justifications for exploring the consequences of neutral effects in communities. The first is to use predictions of neutral models as null hypotheses in tests of more complex processes to explain patterns in community structure (Bell 2001); much as Hardy-Weinberg expectations of genotype frequencies are used as the null expectation to evaluate the operation of evolutionary forces. Obviously, this is a basic tenet of

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inferential science that now has a long history in ecology (Gotelli and Graves 1996).

The second justification is based on parsimony and argues that until mechanisms of niche-differentiation are shown to be necessary to explain patterns in community structure, we should use the simplest models (i.e., involving the fewest mechanisms and parameters) to account for such patterns. The ability of neutral models to generate predictions that are consistent with many important patterns (e.g., rank abundance distributions) is impressive. However, other features of real communities (e.g., spatiotemporal patterns of species turnover [Adler 2004], distributions along gradients [Chase et al. 2005], and patterns resulting from experimental manipulations [Wootton 2005] demand more complicated explanations; see also the review by Chave 2004). Unless neutral models provide parsimonious explanations for all these patterns and their interrelations, parsimony is no justification for abandoning niche differentiation models.

These two justifications necessarily construct a dichotomy between the neutral and niche perspectives. A third justification is the one we find most compelling. It is based on the realization that complex systems (like real food webs) are structured by the interplay of many disparate mechanisms simultaneously. For example, in a relatively “simple” four-species food web, one can simultaneously see the operation of direct predator–prey interactions and indirect effects of both resource and apparent competition (Holt et al. 1994, Leibold 1996, McPeck 1996a). The operation of one mechanism does not negate the operation of another, particularly as more species are added to the system. To us, the important point of considering “neutral” community processes is likewise that they draw attention to additional processes and transient dynamics of groups of ecologically similar or equivalent species embedded in structured food webs and that interact with the rest of the community as essentially one functional group. The critical questions to be addressed do not pit the “niche perspective” against the “neutral perspective,” but rather ask when and to what degree both niche differentiation and equivalence together influence community structure.

Here we evaluate what factors affect the possible evolution of equivalent species in regional biotas, and evaluate the factors that may influence how co-occurrence of such species might be affected at local scales (spatiotemporal scales that correspond to that of individual fitness and population regulation) and at metacommunity scales (interconnected local communities that affect each other’s assembly histories and subsequent dynamics).

#### SUBTLE BUT IMPORTANT DISTINCTIONS

We start by refining and clarifying the meaning of species “equivalence.” Clearly, species must differ in some way or they would not be separate species, and so the strict equivalence of species in all aspects of

phenotypes and ecology is untenable. Coexistence requires that species respond to ecological heterogeneities in different ways, and these differences are usually the result of trade-offs in the abilities of species to interact with various features of their environment (Chesson 2000). We restrict our use of “coexistence” to situations where persistence is indefinite for multiple species and results from mechanisms of niche differentiation (Chesson 2000). We use “co-occurrence” to imply a less restrictive definition in which species are found together regardless of whether persistence is permanent; some co-occurring species will be coexisting with one another, but others may be in the process of being driven extinct by interactions with other species. Thus, species equivalence must be evaluated with respect to the phenotypes that influence their degree of niche differentiation.

The strictest ecological perspective of equivalence is that species differences are completely unrelated to traits that influence any aspect of their fitness or demography, and thus their interactions with the abiotic environment and other species. Molecular systematic studies are providing an ever lengthening list of taxa that were thought to be one species only a few years ago, but are now known to be groups of co-occurring, cryptic species (reviewed in McPeck and Gomulkiewicz 2005). For example, *Hyallela azteca*, an amphipod found in most water bodies across North America, is in fact a cryptic complex of eight species that has existed since the Miocene (Witt and Hebert 2000, Witt et al. 2003). Moreover, most water bodies support multiple species from this complex. Diagnostic characters for these species have not been identified (other than DNA sequences), and yet these cryptic species are reproductively isolated from one another (G. A. Wellborn, *personal communication*). Presumably, the main differences among these cryptic species are reproductive traits. Even in these cases, intraspecific competition for mates could slow per capita population growth in ways that only apply to conspecifics, and could thus serve as modes of niche differentiation (i.e., asymmetries in intra- vs. interspecific effects). However, even though we can imagine mechanisms that would promote their coexistence, the existence of long-standing, cryptically co-occurring species complexes must open the possibility of truly ecological equivalent species embedded in local communities.

Even noncryptic species could be ecologically similar enough to one another to make equivalence an important component of community dynamics. Species may differ in ecologically important traits that influence their fitnesses and demographies, but if these differences are not related to relevant environmental heterogeneities that promote their coexistence, these species are ecological equivalents with respect to coexistence mechanisms and community dynamics. Only phenotypic differences that substantially contribute to promoting coexistence are relevant to identifying ecologically differentiated species. For example, species may show different abilities to consume a particular spectrum of

resources, but if partitioning those resources is not the process that promotes their coexistence (e.g., those resources are not limiting to their population sizes), their relative abundances within and between communities will be governed by their common responses to environmental heterogeneities (i.e., equalizing effects). Coexistence demands the more stringent requirement that species must differ in ecologically important characters that cause differential responses to environmental heterogeneities (i.e., trade-offs) that generate stabilizing effects (Chesson 2000). The mere existence of ecological differences among species, even in traits that influence their fitnesses and demographies, does not belie the fact that those species may be ecologically equivalent with respect to community dynamics.

Moreover, ecological similarity among species may have profound consequences on community dynamics even when species do differ in ways that promote niche differentiation. In general, Chesson (2000) emphasized that the magnitude of niche differences needed to generate coexistence decreases as the overall fitnesses of species become more similar. Thus, even the existence of niche differences among species does not negate the potential importance of ecological similarity/equivalence to structuring overall community dynamics. The niche perspective and the neutral perspective define endpoints of a continuum, and we entertain the possibility that all ecological systems lies somewhere between these endpoints—neither completely neutral nor completely niche structured.

#### WHERE DO EQUIVALENT SPECIES COME FROM?

The prevalence of “neutrality” and its relation to coexistence and consequently to biodiversity will vary with the mechanisms that introduce new species into systems and with the scales over which potential differences act. New species enter systems either via immigration from another system or via speciation within the system under consideration. Even before human-induced biotic mixing became important, immigration of new species among biogeographic provinces had profound consequences for extinction of native taxa and overall community structure (see the lucid and entertaining biological history of North American immigration and emigration in Flannery 2001). Because immigrant species by definition first arose and adapted to the ecological conditions of another system, immigrants are not likely to be ecologically equivalent to any of the natives. Thus, community dynamics induced by invading species are unlikely to have a substantial neutral component.

Because of the hegemony of niche differentiation in our thinking, ecologists tend to focus on speciation modes that produce new species as a by-product of niche differentiation (e.g., MacArthur 1965, Rosenzweig 1978, Pimm 1979). Under ecological speciation, lineages segregate into different niches either sympatrically (e.g., Pimm 1979, Dieckmann and Doebeli 1999) or

allopatrically (McPeck 1996b, Doebeli and Dieckmann 2003), and reproductive isolation arises as a by-product of this ecological differentiation (Schluter 1996, 2000, Coyne and Orr 2004). The classic example of sympatric speciation in *Rhagoletis* flies was accomplished by some lineages that were previously adapted to utilizing hawthorn trees adaptively differentiating to utilize a new host plant, the introduced apple tree (Feder et al. 1988, 1997). Four new *Enallagma* damselfly species resulted from three independent invasions of fishless ponds and lakes during or shortly after the Wisconsin glacialation by rapidly adapting to coexist with large, active dragonflies (McPeck and Brown 2000, Turgeon and McPeck 2002, Turgeon et al. 2005). The great diversity of *Anolis* lizards in the Caribbean archipelago is largely the result of repeated ecological differentiation into the same suite of habitat use niches on different islands (Losos et al. 1998). Clearly, ecological speciation is prevalent, but by definition ecologically equivalent species cannot be produced, because ecological speciation is a by-product of niche differentiation.

However, speciation as a by-product of ecological differentiation is not the only way new species are made; many other modes of speciation can potentially generate ecologically similar or equivalent species. By definition (at least in sexual species), speciation is the process that generates reproductive isolation between two or more genetic lineages. Changes in myriad traits can generate reproductive isolation between lineages, including changes that prevent contact between putative species (e.g., spatial or temporal segregation), changes in mate choice, changes in gamete recognition or compatibility, and offspring viability and fertility (Dobzhansky 1937, Mayr 1942). The evolution of traits that enforce reproductive isolation among lineages are those that cause speciation; speciation does not require ecological differentiation at all.

In many speciation modes, traits conferring reproductive isolation need not be ecologically important at all (Carson 1985). For example, the evolution of mate recognition or pre-zygotic sexual compatibility systems may involve changes in characters that have no ecological consequences whatsoever. Some of the most rapidly evolving proteins in the animal world are gamete compatibility and recognition proteins that only influence whether an egg and sperm will fuse (Rice and Holland 1997). Sexual incompatibility between many insect species involves differences only in genital morphology (e.g., Eberhard 1988), which presumably has little or no influence on how these species avoid predators, acquire resources, combat parasites, foster mutualists, or deal with the abiotic environment. Thus, many of the co-occurring *Enallagma* species appear to be the product of speciation due to sexual differentiation, because these species differ only in adult structures used in specific mate recognition and not in ecologically important traits (reviewed in McPeck and Brown 2000). Speciation by chromosomal rearrange-

ment may have similar effects of generating reproductive isolation without significantly altering ecologically important phenotypes (King 1993).

Speciation via hybridization in many ways offers the most ecologically interesting array of possibilities in this context. Species derived by hybridization events typically have phenotypes that are relatively intermediate to their parental species (Stebbins 1950, Rieseberg 1997), and thus the degree of ecological similarity of the hybrid to other species in the community will depend to a large extent on the degree of ecological similarity of the parental species.

These considerations suggest that the speciation mode of a particular taxon will largely determine the likelihood of ecological equivalence in that taxon. In this regard, many examples of fantastically diverse animal taxa such as African lake cichlids (McKaye 1991, Seehausen et al. 1997, Kornfield and Smith 2000, Turner et al. 2001) and Hawaiian *Drosophila* (Kaneshiro 1988, Boake 2002) are thought to have diversified primarily by sexual selection. Perhaps ecological equivalence among co-occurring species can in part explain their tremendous diversity.

For ecological equivalence to be important, not only must speciation mechanisms produce ecologically similar species, but they must also be introduced into systems in ways that make their persistence over long time scales possible and that make contact between ecologically similar species likely. Thus, some geographic configurations of speciation may not be relevant to considerations of ecological equivalence. For example, speciation via a vicariance event after which the resulting species never come into contact with one another will increase the beta diversity of the regional landscape but poses no ecological quandary to be explained. The ecologically interesting features of such scenarios do not begin until the vicariance barrier is breached and one or both species begin to expand into the other's range. This will be true of all forms of allopatric speciation in which the resulting species have non-overlapping ranges (e.g., dividing a large range into multiple large pieces, peripheral isolate speciation).

In contrast, sympatric speciation will by definition create new species that are interacting with their progenitors immediately. For example, hybridization will usually produce species that must almost immediately interact locally with their progenitors. Other mechanisms that are more likely to produce ecological equivalents can in theory also operate in a sympatric speciation context (Gavrilets and Boake 1998, Gavrilets and Waxman 2002). However, sympatric speciation also implies that the newly created species begins at a substantially lower frequency than its progenitor. Unless this new species either has a fitness advantage and can replace its progenitor or comes into being as a result of ecological speciation and can immediately coexist with its progenitor (Schluter 2000), such species are unlikely to persist for very long.

The paleontological record suggests that the introduction of new species frequently coincides with major climatic events that disrupt the integrity of ecological systems. Vrba (1985) has termed this "turnover-pulse" speciation, to highlight the cycle of extinctions and radiations that occur during these brief periods of upheaval. Periods of climatic change often cause species ranges to shift and fragment (Vrba 1985, Davis 1986, Graham et al. 1996, Hewitt 1996, Bernatchez and Wilson 1998, Delcourt and Delcourt 1991, Coope 1995). The cycles of glacial advances and retreats over the past 2 million years may have driven many species extinct, but may have spawned the radiations of some lineages across the globe (e.g., Lovette and Bermingham 1999, Price et al. 2000, Turgeon and McPeck 2002, Turgeon et al. 2005). New species arise as a result of being fragmented into refuge areas and as lineages expand out of refuges to recolonize deglaciated areas (Hewitt 1996, Bernatchez and Wilson 1998). During these turbulent periods, local and regional biotas are disassembled and reassembled into potentially unique configurations (e.g., Coope 1995, Graham et al. 1996). Here, the problems of establishment and invasion do not affect equivalent species introduced during these periods of upheaval as they do for species entering long-standing systems. New species are not invading an already intact community, but rather the system is reassembled and new species are introduced simultaneously. Thus, we expect species equivalence to be most prevalent in systems that were more severely impacted by recent climatic upheavals.

#### HOW DO SIMILAR SPECIES PARTICIPATE IN COMMUNITY DYNAMICS?

Given that macroevolutionary dynamics may frequently introduce ecologically similar or nearly equivalent species into a system, how are such species likely to affect community dynamics? To date models of community dynamics involving equivalent species focus exclusively on the role of stochastic demography and population regulation on community dynamics and contrast this with relatively simplistic niche theory focused on "stabilizing" processes (e.g., Levins 1968, May 1973). Because niche theory focuses on the local scale and because community assembly dynamics are different when regional effects are considered (see Chase and Leibold 2003, Leibold et al. 2004), this contrast establishes two false premises: (1) that neutral models and niche-based models are mutually exclusive and (2) that niche differentiation is only important at the local scale.

One general result to emerge from niche-based theories focused on local coexistence is that stabilizing aspects of competitor coexistence (i.e., mechanisms that promote a system to return to a particular equilibrium distribution of relative abundances) are enhanced when intraspecific feedbacks are more strongly negative than interspecific feedbacks. These feedbacks depend strongly on the impact that species have on their environment



and consequently on each other (Goldberg 1990, Leibold 1995, Chase and Leibold 2003). Myriad mechanisms can promote coexistence through species differences (see Chesson 2000), including almost the entire array of possible niche axes that one might consider important (see Chase and Leibold 2003). Experiments conducted in controlled situations, such as batch cultures (see Lawler 1998 for a review), chemostats (e.g., Titman 1976, Bohannan and Lenski 2000b), mesocosms (e.g., Wilbur 1997) and in the field (e.g., Gurevitch et al. 1992), support this conclusion. Additionally, numerous studies have identified major patterns in species distributions, particularly along environmental gradients, that are consistent with these predictions (e.g., Whittaker 1975).

However, these stabilizing effects of species differences are often in conflict with another important aspect of competition, namely that similar ecological attributes are often favored among competitors. Chesson (2000) has called these “equalizing” effects to contrast them to the “stabilizing” effects that are highlighted by niche theoretic constructs. Coexisting species should be more similar species to one another than they are to species found under other ecological conditions because they respond similarly to environmental features. Evidence for the importance of these equalizing effects can be found in experimental studies involving species that also show stabilizing niche differences (e.g., Titman 1976, Bohannan and Lenski 2000a).

The important complication is the tension between how organisms affect features of the environment (stabilizing effects) and how organisms respond to those environmental features (equalizing effects). This conflict can be seen in at least two well-studied theoretical approaches to competition. For example, Vandermeer (1975) studied the Lotka-Volterra competition equations:

$$dN_i/dt = N_i r_i (K_i - N_i - a_{ij} N_j) / K_i$$

where  $i = 1, 2$  for species 1 and species 2 to illustrate these tensions. Differentiation between two competing species is summarized by four quantities: the ratio of intrinsic population growth rate ( $r_1/r_2$ ); the ratio of carrying capacities ( $K_1/K_2$ ); the “classical” measure of the strength of interspecific competition ( $a_{12} \times a_{21}$ ) where  $a_{12}$  is the ratio of the effect of species 2 on 1 relative to the effect of 1 on itself; and another measure of interspecific competition ( $b_{12} \times b_{21}$ ) where  $b_{12}$  is the ratio of the effect of species 2 on 1 relative to the effect of species 2 on itself. The species are ecologically equivalent when all these ratios and products equal 1. Algebraic and graphical analyses show that convergence of carrying capacities ( $K_1/K_2$ ) and of intrinsic growth rates ( $r_1/r_2$ ) facilitates local coexistence (Fig. 1). This occurs because these parameters prevent strong asymmetries between the species in their responses to the local environmental template. Divergence in  $a_{ij}$  and  $b_{ij}$  can either facilitate local coexistence (if  $a_{ji} a_{ij}$  and  $b_{ji} b_{ij}$  deviates from equivalence by being smaller than 1) or

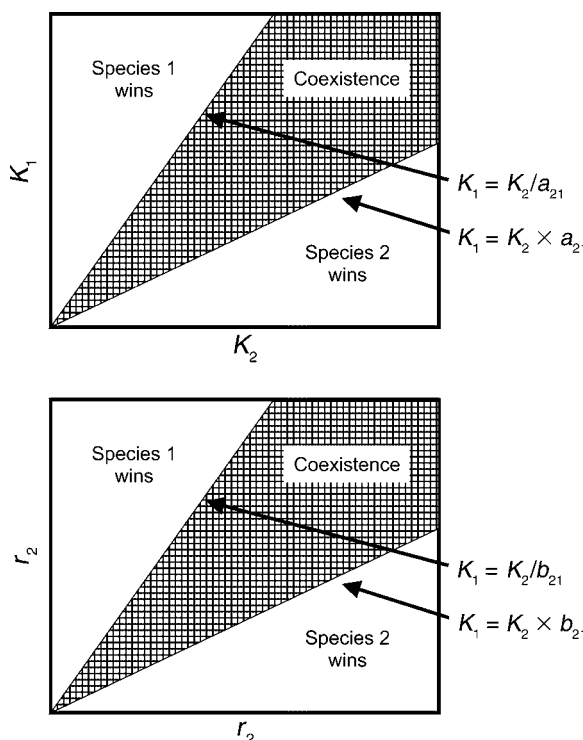


FIG. 1. Parameters for  $K_1$ ,  $K_2$ ,  $r_1$ , and  $r_2$  that allow for stable coexistence of two species assuming that the products  $a_{12} \times a_{21}$  and  $b_{12} \times b_{21}$  are both less than 1. Coexistence is favored at intermediate ratios of  $r_1/r_2$  and  $K_1/K_2$ . If either parameter is altered in one species there must be a corresponding change in the other for continued coexistence so that these parameters maintain their relative similarity. The figure is redrawn from Vandermeer (1975).

hinder it (if these products are larger than 1). In Fig. 1, the products  $a_{ji} a_{ij}$  and  $b_{ji} b_{ij}$  determine the size of the region of coexistence. If the products are less than one, as shown in Fig. 1, the area of coexistence is larger when these products are smaller and thus when species have greater niche differentiation (intraspecific effects are larger than interspecific effects). Coexistence is thus favored by similarity in some parameters ( $K_i$ ,  $r_i$ ) and dissimilarity in others ( $b_{ij}$ ,  $a_{ij}$ ).

This conflict between equalizing and stabilizing factors arises in other formulations of niche interactions as well (MacArthur 1972, Tilman 1982, Leibold 1998). For example, Leibold (1998) examined how interactions mediated via competition for shared resources (shown in Fig. 2), “apparent competition” mediated through shared predators (not shown here), and keystone predation involving both of these interactions (also not shown here, see Leibold 1998) were related to the similarity in effects and responses of two species at the intermediate trophic level. The conclusion was that assembly dynamics would favor their local coexistence if they had similar responses to these factors (i.e., equalizing effects) but that the community stability was decreased if they had similar impacts on these factors

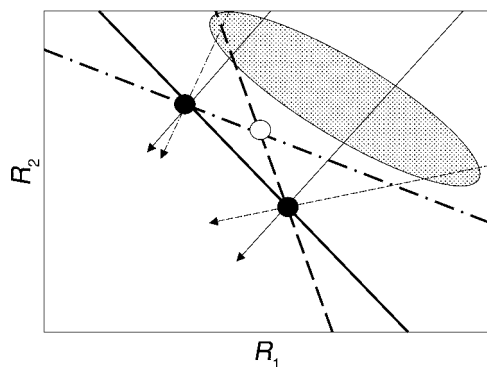


FIG. 2. Coexistence and similarity among three species competing for two resources using explicit consumer resource equations (MacArthur 1982, Leibold 1998). The lines depict zero net growth isoclines (ZNGIs) for three species that differ in their relative abilities to exploit the two resources. The species depicted with the solid-line ZNGI is intermediate between the other two species. The species with a ZNGI depicted with the dot-dash line is a relative specialist on resource 2, and the species with a ZNGI depicted with the dashed line is a specialist on resource 1. We assume that each species also has impact vectors depicted as arrows with corresponding lines as shown, so that the generalist is more similar to the specialist on resource 2 than to the specialist on resource 1. The three circles depict equilibria associated with coexistence of pairs of species. The open circle is an equilibrium in which both specialists coexist, and this equilibrium is invulnerable by the intermediate species (it lies to the upper right of the ZNGI for the intermediate species). The other two solid circles are not invulnerable by the missing species. Thus uninvulnerable species pairs are those that involve coexistence of the generalist with either of the specialists and involve coexistence of the more similar species pairs in this group. The shaded oval depicts a range of environmental conditions in the supply of the two resources assumed to be evenly distributed over these conditions. In a landscape with environmental conditions characterized by such a distribution, the generalist will coexist with the specialist on resource 1 more often than with the specialist on resource 2 because the difference in their impacts on the two resources is greater. Thus coexistence is favored for species that differ more greatly in such impacts if these differences are disassociated from their resource requirements (i.e., their ZNGIs). This general argument holds well in cases where the equilibria depicted in the figure are point attractors such that the steady state dynamics do not involve oscillations or chaotic dynamics. Abrams (1999) has shown that when the steady-state dynamics do involve oscillations driven by destabilized consumer–resource dynamics, the resulting patterns of coexistence do not favor similar species. The reasons are that differences in the nonlinearities that drive the pattern must be large enough to stabilize the interaction that results. Thus, conclusions about similarity and coexistence are in fact complex. Even so, we can hypothesize that coexistence of similar species is possible in a niche-theoretic context but not inevitable. The figure is redrawn from Leibold (1998).

(i.e., stabilizing processes). As in the Lotka-Volterra models, coexistence is favored by similarity in some factors and by dissimilarity in others.

The important insight from these interpretations of niche theory is that ecologically similar species are often likely to coexist, especially when their similarities are primarily related to ecological traits that affect how they respond to the environment. Leibold and Chase (2003)

review some of the evidence that supports this conclusion. In the limit, and as these traits range from being very different to very similar, they suggest a range of dynamics that approach those predicted by neutral models based on the assumption of equivalence among species.

#### EFFECTS OF METACOMMUNITY DYNAMICS ON COEXISTENCE OF SIMILAR SPECIES

In isolated local communities, the stabilizing features of competition are critical for long-term species' persistence and coexistence, because extirpated species cannot recolonize. In contrast, in open systems where local communities are connected by dispersal either to an external species pool (e.g., mainland–island scenarios) or to other local communities (i.e., archipelagos of patch types), species can recolonize patches in which they have gone locally extinct. Consequently, assembly dynamics should be more important to local community structure in such metacommunities.

In the models described above, noninvasive local communities consist of combinations of similar species. As coexisting species become more similar their dynamics should converge on equivalence (sensu Hubbell 2001), where the total abundance of the entire assemblage is regulated as though it were a single species, but the relative abundances of component species change via a random drift process. In a metacommunity, however, such combinations of equivalent species could coexist with other species or species combinations via strong niche differentiation. We have hypothesized just such a community structure for the damselfly assemblages inhabiting eastern North American lakes. *Ischnura* and *Enallagma* damselflies differ from one another in ways that should promote their coexistence according to the growth vs. predation risk trade-off (e.g., Levin 1974, Holt et al. 1994, Leibold 1996, McPeck 1996a): *Ischnura* larvae are better than *Enallagma* larvae at converting food resources into their own biomass, but *Enallagma* larvae are better than *Ischnura* larvae at avoiding their shared predator (McPeck 1996a, 1998, 2004). These differences among the genera would be completely consistent with niche differentiation structuring this assemblage if only one species of each genus were present in a given lake. However, five to 12 *Enallagma* species and two to four *Ischnura* species are typically found locally co-occurring in lakes across eastern North America (Johnson and Crowley 1980, McPeck 1990, 1998, McPeck and Brown 2000). Moreover, species within each genus are phenotypically and ecologically quite similar to one another (McPeck 2004). Within each genus, species may differ in quite subtle ways that promote their coexistence. However, another possibility is that conspecifics are instead nearly equivalent species and because local and regional abundances are huge and dispersal among lakes can recolonize extirpated species, ecological drift that would eventually cause extinctions of some species is exceedingly slow (McPeck and Gomulkiewicz 2005). If this latter case is true, each

genus would essentially operate as a separate functional group within the food web, with the ecological dynamics of the food web regulating the total number of *Ischnura* and *Enallagma* individuals, respectively, and not the abundances of each species separately.

Additionally, in metacommunities with dispersal among patches, each patch may contain sink populations of many species, and this species co-occurrence is facilitated by ecological similarity (Loreau and Mouquet 1999, Amarasekare and Nisbet 2001, Mouquet and Loreau 2002). Such source-sink relations require that patches differ in local ecological conditions, and coexistence at the larger metacommunity level requires patch type specialization. Here, each patch will have one species that would drive all others extinct without dispersal, but dispersal from nearby patches will maintain inferior species in a patch as sink populations. Again, such co-occurrence is more likely and will be more prevalent when species are ecologically more similar or equivalent because the size of the sink population that can be maintained is inversely related to the fitness differences of species relative to the best competitor in each patch. In addition, sink populations of ecologically nearly equivalent species will also depress the abundance of the local competitive dominant species.

Returning to the damselfly example, these complex source-sink dynamics is also a likely mechanism for the persistence of such great diversity. Lakes in a given region clearly differ in many ecological features that influence the fitnesses of both *Ischnura* and *Enallagma* damselflies, even if we restrict our consideration to similar lake types. For example, the same *Enallagma* and *Ischnura* species are typically found at all lakes in a given area with fish as the top predators (McPeck 1990, 1998). But all fish lakes are not identical; they differ in features of their abiotic environment, the spectrum of available resources and their various abundances, the composition and abundances of the fish faunas that feed on them, etcetera, all of which will influence damselfly fitnesses. Presumably in each lake, one *Ischnura* and one *Enallagma* species is the best competitor for their respective functional positions in the food web, but the ecological variation among lakes may favor different species of each genus being the best competitor at its functional position in different lakes. Here, because species within each genus are ecologically so similar, only a small amount of dispersal is needed to keep all species at relatively high abundances in all lakes in a given region (McPeck and Gomulkiewicz 2005).

Furthermore, additional issues emerge for metacommunities, namely the existence of species in the broader metacommunity depends on traits that affect dispersal and colonization as well as the conventional niche-theoretic traits. For equivalence to hold at the metacommunity scale as hypothesized in the purely neutral model (Hubbell 2001), species must also be equivalent in their dispersal abilities, and if this is not so, species may either go extinct from the metacommunity much faster than predicted by

the neutral model or they may coexist at either the local or regional scale via colonization-competition trade-offs (Tilman 1994, see Amarasekare 2003 for a general review). Again theory on these issues indicates that coexistence at larger metacommunity scales, mediated via such processes, favors species that do not differ too greatly in their ecological attributes (Amarasekare and Nisbet 2001, Mouquet and Loreau 2002, Amarasekare 2003). Thus, when dispersal is included in a metacommunity context, the co-occurrence of species becomes more likely as species become more similar to one another, and the recognition of these neutral processes has implications for interpreting patterns of absolute and relative abundances. The resulting communities will have many attributes predicted by a purely neutral context, including fitness equivalence at various spatial scales, high similarity in responses to local environmental conditions, and a significant role for stochastic drift in regulating abundances. However, other elements of their basic structure will differ strikingly from predictions of neutral models in other respects, such as strong overarching food web structure, shifts in species abundances along environmental gradients (e.g., Whittaker 1975) and species association patterns (Gotelli and Graves 1996, Leibold and Mikkelsen 2002). The amalgamated properties of niche and neutral mechanisms are what we need to understand.

#### HOW WILL ECOLOGICALLY SIMILAR SPECIES ADAPT TO ONE ANOTHER?

Given that very similar species can evolve, and given that ecological dynamics may permit their co-occurrence both locally and regionally, we must then ask how species will coevolve under these types of ecological scenarios to alter the likelihood of coexistence of similar species. Our intuition tells us that competing species should evolve differences to reduce the effects of interspecific competition for a given functional position in a food web—natural selection should favor the divergence of co-occurring *Enallagma* species to reduce interspecific competition. The ecological dynamics of the system may favor this coevolutionary response because reducing the magnitude of interspecific effects relative to intraspecific effects will make the system more stable, and as a by-product increase the likelihood of their coexistence. Such coevolutionary responses fall under the general rubric of “character displacement.” Many well-established empirical examples of character displacement have been demonstrated (see review in Schluter 2000). However, the existence of character displacement examples does not imply that evolution will invariably favor the divergence of competing species. Natural selection generated from ecological dynamics in some cases may push competing species to become more similar to one another, thus increasing the importance of equivalence to overall ecological dynamics.

In fact, theoretical studies suggest that general rules cannot be stated for the outcome of competitor coevolution for various types of functional slots in food



webs. Coevolutionary character change among resource competitors has been well studied theoretically (e.g., Lawlor and Maynard Smith 1976, Slatkin 1980, Abrams 1986, 1987, Taper and Case 1992, Geritz et al. 1999). Although many of these studies found that character (and species) divergence was a common outcome, many alternate but realistic assumptions instead lead to character convergence (Abrams 1986, 1987, 1990). Since these initial studies of resource competitors, Abrams has made detailed theoretical studies of species competing for many types of functional positions in food webs. As with resource competitors, Abrams (2000) has shown that character displacement is not the exclusive outcome among "apparent" competitors (species that are fed upon by a common predator; see also Brown and Vincent 1992) or among species that are simultaneously resource and apparent competitors (Abrams and Chen 2002, Abrams 2003). In fact, the likelihood of divergent coevolution depends critically on specific model assumptions (Abrams and Chen 2002). Moreover, when competing species are simultaneously engaged in multiple types of interactions, adaptive coevolution can cause species to converge in one set of traits (e.g., those that influence resource acquisition abilities) and diverge in others (e.g., predator avoidance traits) and converge in overall fitness as well (Abrams and Chen 2002). Evolutionary dynamics of niche relations can be complex (Odling-Smee et al. 2003). Thus, our intuition about evolutionary responses is often flawed, particularly when frequency- or density-dependent selection predominates (Bürger 2002). We may expect that coexisting species that are similar may sometimes converge further towards becoming equivalent, but they may also often diverge to show biologically significant niche differentiation. Consequently, it seems unlikely that entire assemblages of species will evolve to be equivalent even though subsets of species may.

#### TESTING THE NEUTRAL AND COEXISTENCE PERSPECTIVES

How might we tell whether drift processes are important to structuring natural communities? The current focus on abundance distributions is severely limited, because such patterns cannot discriminate among the multiple alternatives that can generate the same patterns. Instead what we need are methods that can identify which species combinations are most likely to act as equivalents. One suggestive method, based on neighborhood analyses is described by Uriarte et al. (2004). In this case fitness traits associated with individual plants are regressed on general evaluations of competition (e.g., neighbor density and sizes, as well as target size) as well as taxonomically related measures. In a data set of plant abundances for Barro Colorado, some species appeared to show no sensitivity to the taxonomic identity of their neighbors (according to this criterion), whereas other species did generally show greater sensitivity to more closely related species. Like all correlative approaches, confounding variables and

the network of causation are ultimately problematic. However, such correlative analyses are significant first steps, and these techniques are great improvements over other approaches because they specifically recognize the potential joint dynamics of niche and neutral processes.

Ultimately, searching for pattern in correlative studies is not enough; manipulative experiments are needed to directly evaluate the dynamics of real communities that account for the joint action of niche and drift processes. Although myriad coexistence mechanisms can potentially operate on many spatial and temporal scales, their existence should be identifiable by signature characteristics (reviewed in Tilman and Pacala 1993, Chesson 2000). In general, all coexistence mechanisms share two properties: (1) they produce density-dependent demographic rates (survival, growth, fecundity) that change along environmental gradients (Chesson considered mainly competing species and termed this "covariance between environment and competition"), and (2) species differ in how the form and strength of these density-dependent demographic rates change along these environmental gradients (Chesson 2000). These differences in species' responses along environmental gradients are what promote their coexistence (Chesson and Huntly 1997).

In contrast, as species become ecologically more similar to one another (i.e., equalizing effects become larger), both their local fitnesses and how those fitnesses change along environmental gradients converge. As a result, ecological factors will regulate the summed total abundance of all equivalent or nearly equivalent species and not the abundance of each species individually. Thus, the relative abundances of equivalent species on local and regional scales will not be influenced by changes in environmental conditions (Hubbell 2001).

These differences in the signatures of stabilizing and equalizing effects suggest straightforward observational and experimental studies to quantify the contributions of niche and drift processes. Consider two species, A and B, that co-occur in many patches across the landscape, and whose relative abundances vary among patches. Furthermore, imagine that these patches are not all identical, but rather have numerous measurable ecological gradients (e.g., physical and chemical gradients, gradients in various resources, predators, mutualists, diseases, etc.) among them. If local and/or regional processes promote A and B's coexistence, we should be able to demonstrate various relationships. First, their absolute and thus their relative abundances should negatively covary along some gradient(s) among the patches (i.e., trade-offs to environmental gradients are what promote coexistence [Chesson 1991, 2000]). Also, perturbations of their relative abundances will alter their fitnesses because they will no longer be at their demographic equilibria. So for example, imagine a scenario in which A and B are regulated by the local ecology in a patch to coexist, with A at a much higher relative abundance than B. If we perturb A's relative

abundance to low levels in this patch while holding A and B's total abundance constant, A should have higher fitness in this treatment relative to an unperturbed control, and B should have lower fitness. These fitness differences result from the species being perturbed from their equilibrium abundances. In contrast, if A and B are equivalent, their relative abundances should show little or no correlation with underlying gradients, whereas their absolute abundances may positively covary with some gradients (and in particular their summed absolute abundance). Moreover, experimentally perturbing their relative abundances will have no effect on fitness; their fitnesses will only vary as their summed total abundance is perturbed.

Because population regulation is an ecological process, testing for coexistence and neutral processes regulating communities is in the end a search for ecological causes. However, our evolutionary considerations do suggest that ecologically similar species are more likely to be more closely related to one another, and to have resulted from speciation mechanisms that should result in little or no necessary ecological divergence. Understanding the phylogenetic relationships among species may therefore greatly aid in identifying species that may be ecologically similar, but the ultimate testing requires an understanding of the ecological processes shaping absolute and relative abundances across the landscape and through time.

#### CONCLUSIONS

Niche differentiation has long been the focus for explaining biodiversity. The idea of limiting similarity was axiomatized in the very roots of the development of the niche concept (Grinnell 1917) and is an ingrained part of ecological thinking. Even though evidence suggesting that similar species co-occur in nature has long been recognized (e.g., congeners tend to coexist much more frequently than expected by chance (Pielou 1978) this evidence has often been dismissed as being due to nonequilibrium situations. However, one critical issue emphasized by the development of neutral theory is exactly that such non-equilibrium dynamics may be pervasive in some features of communities containing very similar species (McPeck and Gomulkiewicz 2005). With this perspective, patterns such as the co-occurrence of congeners take on a new meaning and significance (damsel flies as a case in point, and cryptic species in general). Consequently, many of the related ideas about community structure are also likely to warrant reevaluation. Nevertheless, too strong a focus on neutral dynamics to the exclusion niche driven dynamics is also unwarranted. Consider for example the effects of biodiversity on ecosystem attributes. Although redundancy is seen as a positive aspect of species diversity that buffers change in ecosystem attributes, niche based models of community structure were thought to be incompatible with strongly redundant effects of biodiversity. To the degree that equivalent species do co-

occur in local communities, species redundancy influencing ecosystem attributes may well be dependent on both niche and neutral processes playing interactive roles.

The same is likely to hold for many other questions that relate biodiversity to ecological processes. In all such cases, the importance of considering neutral models is not as a parsimonious foil against which niche explanations are judged, but rather because they identify a set of mechanisms that interact with previously well studied mechanisms of niche differentiation in important ways. Their contrast may have served a dialectical purpose that has drawn attention to the need to consider neutral dynamics but we believe the time is ripe to move away from seeing these processes as antagonistic. Controversies such as this arise because intelligent researchers have found evidence to think that the different perspectives exist or predominate in different systems. Dichotomies do sharpen the differences between alternative processes, but dichotomies are ultimately fettering to our understanding of how those processes may operate in the real world. Similar to previous dichotomies in ecology such as "competition vs. predation" and "top-down vs. bottom up" propositions about community structure, meaningful insights will be made when the various perspectives are synthesized.

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