

Towards a really unified theory for metacommunities

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Introduction

Traditionally, community ecologists assumed that species differ in some aspects of their traits or responses to the environment (i.e. their niches), which allow them to coexist in the same habitat (Hutchinson 1957, 1959). Recently, Hubbell (2001) and others (e.g. Bell 2001, 2003) have suggested that this view is inadequate to explain the diversity often observed in speciose systems. For example, hundreds to thousands of tree species live in tropical forests, which only have a handful of limiting resources such as water, light, and a variety of macro- and micronutrients. Such high diversity, with so few resources, they argue, cannot be explained by niche theory.

As an alternative to the traditional niche theory, Hubbell (2001) developed a neutral theory of community structure (see also Caswell 1976; Hubbell 1979; Hubbell & Foster 1986; Bell 2000, 2001, 2003; Chave & Leigh 2002; Chave 2004). In the neutral theory, patterns of species diversity, relative abundance, and composition are primarily a function of the size of the metacommunity, the dispersal rate of organisms within the metacommunity, and the rates of generation (speciation) of new species (Bell 2001; Hubbell 2001; Chave 2004). Because species are assumed to be identical ecologically, Hubbell termed his a 'neutral theory', by direct analogy to neutral genes in population genetics. Hubbell further termed his theory 'unified' in that it is simultaneously able to predict diversity and relative abundance of organisms in a locality, as well as biogeographic patterns of species composition.

In this essay, I overview the key assumptions (inputs) required and the insights (outputs) that can be gained from each framework. While a complete discussion of all of the assumptions and predictions of these models is beyond the scope of this essay (but see Chase *et al.* 2005), a caricature is presented in Table 1. At the outset, the reader will notice from Table 1, the critical issue I wish to emphasize in this essay: The neutral theory is valuable in its simplicity in inputs, but suffers by the limitation of its outputs. Alternatively, niche theory is less elegant (more complex) by having many more inputs, but can provide much richer insights (outputs).

Despite the neutral theory's successes at predicting some patterns seen in natural communities (Hubbell *et al.* 1999; Condit *et al.* 2000, 2002; Bell 2001, 2003; Hubbell 2001; Volkov *et al.* 2003), other studies have

found patterns less consistent with its predictions (Condit *et al.* 2002; McGill 2003; Magurran & Henderson 2003; Clark & McLachlan 2003; Tuomisto *et al.* 2003; Gilbert & Lechowicz 2004). In addition, several recent studies have shown that similar patterns can be generated from neutral and niche models (Chave *et al.* 2002; Mouquet & Loreau 2003; Wilson *et al.* 2003; Chave 2004; Chase *et al.* 2005). Thus, the jury is still out on the value of the neutral *vs* niche approaches, and which is better supported by empirical data.

In the following sections, I overview a contemporary view of the niche theory, and discuss several issues in community ecology that can not be addressed specifically by the neutral theory. I conclude with a brief discussion of the issues that must be addressed to achieve a synthesis between niche and neutral approaches.

A CONTEMPORARY VIEW OF NICHE

Proponents of the neutral theory claim that niche theory is inadequate because the number of species, particularly in speciose ecosystems, is far greater than the number of limiting resources that niche theory assumes they must partition (Bell 2001, 2003; Hubbell 2001). However, modern niche theory recognizes a variety of factors that influence patterns of community structure other than just consumable resources (for more detail, see, e.g. Tilman 1982; Chesson 2000; Amarasekare 2003; Chase & Leibold 2003; Kneitel & Chase 2004). I briefly describe these below:

Extrinsic temporal variation. Species can coexist indefinitely in temporally variable environments if they trade-off in their response to different conditions (e.g. weather), and they can persist through unfavourable periods (e.g. through long-lived adult stages or seed-banks) (e.g. Chesson 2000). A similar coexistence mechanism occurs when species differ in their susceptibility to disturbances (e.g. some stressful or mortality event) and their competitive ability (e.g. Shea *et al.* 2004).

Intrinsic temporal variation. Organisms themselves can create temporal variation, which in turn can allow coexistence. For example, if consumers cause their resources to cycle, and species specialize on different parts of the temporal sequence (i.e. one species is favoured when resources are common and the other species is favoured when resources are rare), they can coexist by being favoured at different times (Armstrong & McGehee 1976; Huisman & Weissing 1999; Abrams & Holt 2002).

Extrinsic spatial variation. In models of resource competition, many species can coexist on two resources

Table 1. A comparison of the neutral and niche models, listing the key assumptions, inputs and outputs of each. This is not meant to be an exhaustive list, and merely shows some of the key inputs and outputs of each

	Neutral	Niche
Key Assumption	No differences among species	Trade-offs prevalent
Inputs	Metacommunity size Speciation rate Dispersal rate	Spatial heterogeneity Intrinsic Extrinsic Temporal heterogeneity Intrinsic Extrinsic Spatial configuration Interactions in the food web
Outputs	Rank–Abundance Diversity Area Speciation Dispersal Compositional turnover Space	Rank–Abundance Diversity Area Several types of heterogeneity Food web structure Compositional turnover Space Environment Response to environmental change Diversity changes Composition changes Invasive species Effects of and on diversity Effects of and on composition Ecosystem function Effects of diversity Effects of composition

so long as there is spatial variation in the local ratios of those two resources and species vary in their performance on different resource-ratios (Tilman 1982). Many species can also coexist on few resources when they vary in how they utilize their environment; some responding to localized resources (fine-grained) and others responding to more dispersed resources (coarse-grained) (Ritchie & Olff 1999).

Intrinsic spatial variation. When organisms trade-off in their ability to consume resources to low levels and to find new patches, a spatial mosaic of patch quality can be created which allows species to coexist on one resource (e.g. Richards *et al.* 2000). Competitively similar species can also coexist on a single resource by intrinsically generated spatial aggregation. This aggregation can be behavioural if individuals show a bias towards being near conspecifics (e.g. Zhang *et al.* 2004) or a result of differing dispersal probabilities and segregation if dispersal is localized (Murrell & Law 2003).

Space as a resource. When space itself is a resource, ‘regional trade-offs’ can allow species to coexist if they trade-off their ability to compete for resources in a patch and colonize empty patches (Kneitel & Chase 2004). For example, Tilman (1994) showed theoretically that a large number of species can coexist in a region so long as there are always open patches created by death or disturbances, and the species trade-off in

their relative competitive ability and their ability to colonize patches.

Other species (enemies, mutualists) as limiting factors. Predators can facilitate coexistence among their prey if there is a trade-off in the prey’s ability to compete for resources and avoid predation (e.g. Paine 1966; Leibold 1996). Similarly, predators can facilitate coexistence if there is frequency dependence of predator attack on prey species as they become more common (Janzen 1970; Connell 1971). Finally, specialist predators can facilitate any number of prey species as long as each predator limits its prey species (Grover 1994). Although much less studied, trade-offs between attracting mutualists (e.g. mycorrhizal fungi, pollinators) and competing for resources may also create opportunities for local coexistence (see, e.g. Palmer *et al.* 2003).

Interactions among the factors. All of the factors I discussed above (and others) can interact with one another. This creates a rich milieu of possible interactions and outcomes and the number of species that can coexist, both locally and regionally, can be quite high (see, e.g. Shurin & Allen 2001; Mouquet & Loreau 2002, 2003).

OCCAM’S RAZOR: NEUTRAL VS. NICHE

Above and in Table 1, I emphasized that the value of the neutral theory is in its simple structure, whereas niche theory is much more complicated. Yet both models often make similar predictions for at least some patterns. One way to deal with the fact that multiple models can predict the same patterns is to invoke Occam’s razor, or parsimony, which argues that when multiple models predict the same pattern, one should accept the one with the simplest plausible explanation. Indeed, this is exactly what Hubbell (2001) has argued to favour his neutral theory over more complex (i.e. more parameters) niche-theories. This is certainly true if one were to consider only one pattern, such as rank–abundance curves (e.g. Volkov *et al.* 2003). However, because neutral and niche models can make disparate predictions on other patterns in natural communities, studies with multiple empirical patterns will allow for better tests of neutral vs niche models.

Data are available from tropical forests that might allow such tests. For example, Volkov *et al.* (2003) used a very detailed dataset of tropical forest trees on Barro Colorado Island (BCI), Panama to show that the neutral theory’s predicted zero-sum multinomial appears to show a significantly better fit to empirical data of rank–abundance relationships than a log-normal relationship (but see Etienne & Olff 2004). If this were the only pattern available, we might invoke parsimony to accept the neutral theory over more complex niche-based theories that can also predict a rank–abundance shape indiscernible from the zero-sum multinomial (Chave *et al.* 2002; Mouquet & Loreau 2003; Wilson *et al.* 2003). However, data from BCI (as well as other neotropical areas) on species composition along spatial

gradients by Condit *et al.* (2002) found that the neutral theory's predictions were upheld at relatively small, but not at larger, spatial scales. Other studies in tropical forests have also found that patterns in species compositional variation are more consistent with niche-based process rather than neutral processes (e.g. Tuomisto *et al.* 2003). Thus, statistically to compare the neutral *vs* niche theories, it is necessary to determine whether the amount of variation explained by the more complex niche models is large enough to justify its use (Hilborn & Mangel 1997). Such a test would be interesting, but is beyond the scope of this essay.

WHAT THE 'UNIFIED NEUTRAL THEORY' DOES NOT UNIFY

Even if the neutral theory is preferred over niche theories in predicting some patterns because of its simplicity, the neutral theory cannot address a wide variety of questions that are of great importance to community ecologists as well as conservation biologists, which I overview here.

The role of fragmentation and environmental change. The neutral theory predicts how variation in habitat area and dispersal rates will influence community patterns; as such, it can make predictions about some of the effects of habitat fragmentation. However, fragmentation disproportionately influences species based on their traits (Henle *et al.* 2004). For example, predators often require larger areas than their prey, and might be more prone to extinction following fragmentation. Likewise, even within a trophic level, if species differ in their ability to compete in patches and to colonize new patches, then they will be differentially affected by habitat fragmentation (Tilman *et al.* 1994; Mouquet & Loreau 2003). As the neutral theory disregards differences in species traits, it can say little about how fragmentation will differentially alter the composition of species, as well as their interactions with other species in the community.

It is becoming widely recognized that other anthropogenic global changes such as temperature, carbon dioxide, nitrogen deposition, acid deposition, and variation in weather (e.g. El Niño events) can directly influence species abundances, composition, and diversity and can indirectly influence species interactions. A well-known example is that of increased nutrient (e.g. nitrogen and phosphorus) inputs to both terrestrial and aquatic ecosystems. Such inputs favour those species that are able to maximally respond to high nutrients, and those species can then dominate the rest of the community and decrease overall diversity (e.g. Tilman 1982). The neutral theory predicts stochastic but not directed shifts in composition through time. Clark & McLachlan (2003) used long-term variation in temperate trees (using a paleorecord of pollen thousands of years old) to compare these hypotheses, finding evidence in support of the ideas of niche rather than neutrality (but see Volkov *et al.* 2004 for criticisms

of those analyses). Further studies comparing the actual temporal shifts in species composition after an environmental change against the neutral theory's predictions would be enlightening.

Invasive species. Invasive species are one of the greatest threats to biodiversity, along with habitat destruction and global change (e.g. Williamson 1996). While the majority of exotic species introductions fail (i.e. the species does not establish), and many more result in relatively innocuous establishments (i.e. the species remain relatively rare), some become very dominant, particularly in disturbed habitats. A great challenge of community ecology is to determine what makes certain species invasive and certain communities invulnerable (Shea & Chesson 2002).

A reasonable approach might be to ask whether the patterns of domination by a few species and extinction of most species in a community (as is seen with invasive species) can be predicted by the neutral theory. In fact, this seems plausible, as the neutral theory makes similar predictions regarding many rare (and extinct) and few common species. If one could estimate the number of exotic species that fit into each category (extinct [did not establish], rare, common), a comparison with the neutral theory's predictions could be made. However, studies have shown that a species' traits may correlate with its ability to invade a community (Rejmanek & Richardson 1996). Likewise, the invasibility of a community may depend on the types of species present and how similar the traits of these species are to the traits of the invader (e.g. Ricciardi & Atkinson 2004). Furthermore, many invasive species may thrive because they lack natural enemies in their new habitats (the 'enemy release hypothesis'; Keane & Crawley 2002; Colautti *et al.* 2004). In addition, many of the invasive species with the greatest impact on their natural communities are predatory species, particularly in depauperate communities (e.g. Williamson 1996). Because the neutral theory does not consider species traits, or the role of enemies in multiple trophic levels, it cannot address what role these may play in determining which species will become invasive, which communities will be invaded, and what the impact of invasive species will be.

The role of species in ecosystem functioning. 'Ecosystem functioning' is a catch-all term that describes numerous processes, including primary productivity, nutrient cycling, and decomposition rates, and it has become an important concept in the conservation of ecosystems and the services they provide (e.g. Kinzig *et al.* 2002; Loreau *et al.* 2002). Although contentious, particularly regarding the mechanisms, studies often find that the ecosystem functioning increases with increasing species diversity (e.g. Kinzig *et al.* 2002; Loreau *et al.* 2002). A mechanism frequently invoked to explain this relationship is that species differentially utilize the environment around them (i.e. they have different niches), and that with increasing diversity, more of the available resources are utilized and overall

functioning increased (e.g. Tilman *et al.* 1997). Studies also often find an important role of the composition of species (i.e. which species are present) in the functioning of ecosystems (e.g. Downing & Leibold 2002). Because the neutral theory assumes that space is the only limiting factor and that all species are functionally equivalent, it cannot make predictions about the role of species in ecosystem functioning.

Conclusions

Hubbell (2004) has criticized a recent attempt at synthesizing current ideas of the niche (Chase & Leibold 2003) for what it lacks, in particular dispersal limitation and evolutionary insights. He is right; concepts based on niche theory still have a long way to go. However, there have been a number of recent advances that have explicitly incorporated dispersal into niche-based models (e.g. Tilman 1994; Mouquet & Loreau 2002, 2003; Amarasekare 2003; Kneitel & Chase 2004). In addition, within a niche-based framework, ecologists are linking local-scale processes and species interactions with larger-scale processes of speciation and extinction (e.g. Webb *et al.* 2002; Ricklefs 2004). I believe we are on our way to creating a framework that incorporates key elements of both niche and neutral theories; perhaps analogous to the 'nearly neutral' theory of molecular evolution. Specifically, a synthetic view recognizes that species differ in their traits, both with regards to limiting factors and space itself, and that the dispersal limited processes critical to the neutral theory can also be important.

In its current iteration, ideas based on the niche are somewhat inelegant compared to the neutral theory's simplicity, as they are often rather clunky and contingent (but see, e.g. Ritchie & Olff 1999; Wilson *et al.* 2003). Adding issues of dispersal makes them even more complex (Chave *et al.* 2002; Mouquet & Loreau 2003). However, I argue that the cost of having a somewhat less elegant framework from which to start – ideas based on niche in this case – are outweighed by the variety of issues and questions in community ecology that niche theory can address but the neutral theory can not. In particular, niche theory can play a strong role in our understanding of a variety of problems essential to our conservation and management of global biodiversity, such as how communities respond to global change and how and which species become invasive (and what their impacts will be). In addition, theories of niche can inform us of the role that species diversity and composition plays in the functioning of entire ecosystems, which can ultimately influence our own welfare (e.g. Balvanera *et al.* 2001).

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