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Reconciling niche and neutrality through the Emergent Group approach

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Abstract

Both niche and neutral theories have been suggested as potential frameworks for modelling biodiversity. Niche models assume that biological traits represent evolutionary adaptations and define individuals in terms of functional trade-offs. Neutral models assume that all individuals at a single trophic level are functionally equivalent on a per capita basis with respect to their birth, death, dispersal and speciation. The opinion of many researchers is that neutral and niche processes operate simultaneously to generate diversity without knowing how the unification of both models can be achieved. Recently, several theoretical papers have reported evidence on the evolutionary *emergence* of niche structures shaping the *emergence* of groups of similar species. In this way, an Emergent Group is defined as a set of species that have a similar functional niche owing to a convergent ecological strategy. Central to the Emergent Group concept are the assumptions of functional equivalence within and of functional divergence between Emergent Groups. Within an Emergent Group, species richness is subject to a zero-sum rule set by the balance between the rate of individual loss and of immigration. Between Emergent Groups, tradeoffs such as seed size/seedling competitivity, investment in reproductive system/investment in vegetative systems or competitive ability/predator invulnerability are cornerstones of the evolutionary divergence. Delineating Emergent Groups amounts to reaching a compromise between maximizing niche differentiation (i.e. maximizing differences in functional tradeoffs) between Emergent Groups and maximizing neutrality within Emergent Groups. Up to now, the Emergent Group concept has been mostly proposed by theoretical scientists but it should be tested by empirical ecologists. The way in which niche and neutral models could be combined provides a profitable opportunity for theoretical and empirical scientists to collaborate fruitfully.

Keywords: Biodiversity; Ecological equivalency; Biological traits; Neutral theory; Niche differentiation; Redundancy

Introduction

Both niche and neutral theories have been suggested as potential frameworks for modelling biodiversity. Both theories capture something fundamentally correct about the assembly, dynamics and structure of biological communities and both theories have strong, convinced supporters as well as equally strong detractors. The cornerstone of the debate lies in the relative importance of biological traits (functional and life-history traits) *versus* stochasticity in shaping species abundance and diversity patterns. Niche models assume that biological traits represent evolutionary adaptations

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to the abiotic and biotic environment and define species in terms of combinations of various traits mostly related to resource uptake *s.l.* and reproductive strategy *s.l.* (Pachepsky et al., 2001). In this way, habitat heterogeneity allows the coexistence of multiple species because species better at dealing with one environmental factor may be worse at dealing with another (Chesson, 2000). On the other hand, neutral models assume that all individuals at a single trophic level are functionally equivalent on a per capita basis with respect to their birth, death, dispersal and speciation. These models do not assume that all species should be identical in all their biological traits but that differences in their traits are not linked with their per capita demographic rates (i.e. neutrality is defined at the individual level, see p. 6 in Hubbell, 2001). In this way, patterns of species abundance solely emerge because of stochastic drift.

Neutral models surprisingly capture the most widely studied patterns in community ecology, i.e. rank-abundance, species–area and species–turnover relationships. Up to now, there are at least 10 different neutral models proposed (reviewed in Chave et al., 2002; McGill et al., 2006b) mainly differing in the zero-sum assumption (i.e. the same number of individuals in the local community at every time step or not), in the metacommunity concept (i.e. a set of local communities that are linked by dispersal of multiple interacting species or one local community interacting with one metacommunity) and in modelling techniques (analytical or simulations). Many tests of neutral models have focused on attempts to highlight differences between the goodness-of-fit of expected and observed abundance distributions (Holoyak and Loreau, 2006; McGill, 2003; Wootton, 2005) or to detect the distance decay of similarity between local communities (Dornelas et al., 2006), especially when local environmental variations and distances are decoupled (Gilbert and Lechowicz, 2004). Some authors have overwhelmingly rejected neutrality in its undiluted form (Alonso et al., 2006). However, most empirical tests have failed to produce statistically convincing procedures (McGill et al., 2006b) and an observation emerging from several studies is that several neutral as well as non-neutral models may produce the same few diversity patterns (Bell, 2000; Chave, 2004; Mouquet and Loreau, 2003). Therefore, the current attention on abundance distributions is intrinsically limited because such studies cannot discriminate among the underlying models (Chave et al., 2002).

This review attempts to explain why the Emergent Group concept (developed in the following) could be a useful approach to synthesize niche and neutral theories into a general framework. To achieve this, I begin with a review suggesting that a possible reconciliation has emerged from several recent theoretical papers. I then discuss some methodological issues and the major underlying assumptions of the Emergent Group approach: the functional redundancy and the functional divergence. I end with suggestions for future empirical investigations and concluding remarks.

How a possible reconciliation has emerged

One facet of the neutral theories that has received very little attention is that of the assumptions regarding the delineation of the local community to which neutrality applies. Hubbell (2001, p. 6) claimed that functional equivalence applies to a group of trophically similar sympatric species that actually or potentially compete in a local area for the same or similar resources. This definition is substantially different from equivalence often assumed by community ecologists when they aggregate species into trait-based groups for data analysis. Indeed, most community ecologists believe that a species should more strongly compete with a species that is more similar to itself because species having the same biological traits have similar functional niches and carry out similar functional roles (Hooper et al., 2005). This can be linked with the widespread idea that functionally equivalent species cannot stably coexist in the long term (Loreau, 2004), an idea derived from traditional niche-assembly theories based on the Lokta–Volterra competition model. However, using a similar competition model and placing a large number of species at random positions on a niche axis, Scheffer and van Nes (2006) have recently highlighted an emerging (but transient) pattern of self-organized groups that contain several coexisting species having a similar functional niche. While the degree of functional differentiation (distance between groups) depended on the species niche width, the relative abundance of species within a niche was determined predominantly by chance. Independently, Gravel et al. (2006) also showed that the mechanism of competitive exclusion tends to create a regular spacing of functional niches even if their results suggest that a high level of immigration may prevent the establishment of such a limiting similarity. These works confirmed the earlier study of Bonsall et al. (2004) that illustrated how the interplay of ecological and evolutionary processes can drive niche partitioning, and at the same time generate species diversity within a niche. It may thus be expected by now that among coexisting species of a given local community, some may converge towards becoming functionally equivalent while others diverge to show niche differentiation. This idea has long lacked empirical support. In a recent experiment, Fukami et al. (2005) reported evidence to support the idea that community assembly is deterministic in the general composition of trait-based species groups but historically contingent on the species composition within groups. In other words, abiotic and biotic conditions determine the available functional