

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 competitiveness, 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.

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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 ap-

proach: 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 Lotka–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

niches and therefore the trait-based groups that can fill them while the species composition of the trait-based groups is stochastically determined by the history of species arrivals. The fact that the relative abundances of trait-based groups of species converged during succession while the species composition remained historically contingent indicates that (i) deterministic non-neutral rules govern assembly between trait-based groups of species and (ii) the mechanism of species coexistence within trait-based groups is likely neutral.

The Emergent Group approach

As we have increasing evidence for the evolutionary ‘emergence of niche structures and limiting similarity’ (Bonsall et al., 2004) shaping the ‘emergence of groups of similar species’ (Scheffer and van Nes, 2006), the term ‘Emergent Group’ is a good candidate to name a group of species that are sufficiently similar to behave neutrally. Fortunately enough, Emergent Groups were earlier defined by Lavorel et al. (1997) as groups of species sharing similar combinations of biological traits reflecting the compromise solution between adaptive responses and evolutionary constraints. In this way, an Emergent Group is defined as a set of species that have a similar functional niche and, therefore, have convergent ecological strategies (Hérault and Honnay, 2005). Of course, species belonging to an Emergent Group may differ in some traits, which are legacies of their evolutionary history, but if these differences are not directly linked to environmental variables that mediate their functional niches and to dispersal rates that mediate their neutral behaviour, these species are ecological equivalents with respect to community dynamics.

The concept of Emergent Group explicitly assumes neutrality among species within and niche differentiation between Emergent Groups. In this way, Emergent Groups differ (i) from phylogenetic groups as phylogenetic groups only reflect evolutionary constraints while Emergent Group also take into account ecological convergence, (ii) from Guilds as Guilds group species on the basis that they use the same resource (Blondel, 2003) and (iii) from Functional Groups as Functional Groups mostly refer to classifications based on whether species respond to a specified perturbation using the same biological mechanisms (Gitay and Noble, 1997). The ‘emerging’ question is now: how Emergent Groups should be delineated, given a particular pool of species? If we can list the basic potential challenges faced by plants, then we should be able to list the basic biological traits involved in these challenges. These traits should be good candidates for delineating Emergent Groups. Basically, challenges for long-term survival are dispersal

and persistence (Weiher et al., 1999). Indeed, to counterbalance random (or not) local extinctions, plants need to disperse to other local communities, and once established they need to persist (Hanski and Ovaskainen, 2000). An Emergent Group classification of species therefore acknowledges biological traits involved in persistence and dispersal (Hérault et al., 2005; Weiher et al., 1999). Persistence depends on tolerating changes in resource availability *s.l.*, tolerating competitors or predators and tolerating acute or chronic disturbance. Dispersal has a spatial and a temporal dimension. Dispersal in time is obviously associated with propagule longevity. Dispersal in space roughly depends on two properties: the propagule mass and the dispersal mode.

As biological traits associated with dispersal are generally known to have little connection with adult ecophysiological traits that are more linked to persistence (Lavorel and Garnier, 2002), Emergent Groups should be fruitfully delineated using a classification procedure that gives a similar weight to the 2 groups of traits. The first step of all classification procedures is the construction of a similarity matrix (Fig. 1). Gower’s measure of similarity (Gower, 1971) is the best appropriate measure because of its suitability to deal with a mixture of scale types (qualitative, ordinal, ratio, continuous) and its tolerance to missing values (Hérault and Honnay, 2007; Podani and Schmera, 2007). Next, the resulting similarity matrix is clustered through a specified classification procedure (Podani and Schmera, 2006). But now the stumbling block is: How many coexisting species can be packed into an Emergent Group? In other words, what cutting level should be chosen to cluster the species into Emergent Groups? Up to now, answers to these questions are essentially ‘arbitrary’ (Hubbell, 2005). I believe that a pragmatic approach could be to delineate Emergent Groups with the goal of reaching an optimum between (i) maximizing niche differentiation between Groups and (ii) maximizing neutrality within Groups (Fig. 1). (i) Several statistical procedures are already available to prune a cluster tree at a level that optimizes the couple Niche Differentiation–Number of Groups. For example, the Silhouette Index indicates how well each species has been classified into its assigned cluster as compared to the other possible clusters in the trait data set (Rousseeuw, 1987). But other techniques are available: e.g. the KGS penalty function (Kelley et al., 1996) or the use of the BIC (Schwarz, 1978) and/or the AIC (Akaike, 1974) followed by a test of the ratio change in distances between two successive clustering steps (Chiu et al., 2001). (ii) Maximizing neutrality implicitly means that tools to test the neutral theory are available. An adequate test should include an evaluation of its basic assumptions and its ability to fit empirical data compared to other models. But we know that the latter is difficult to test because species abundance

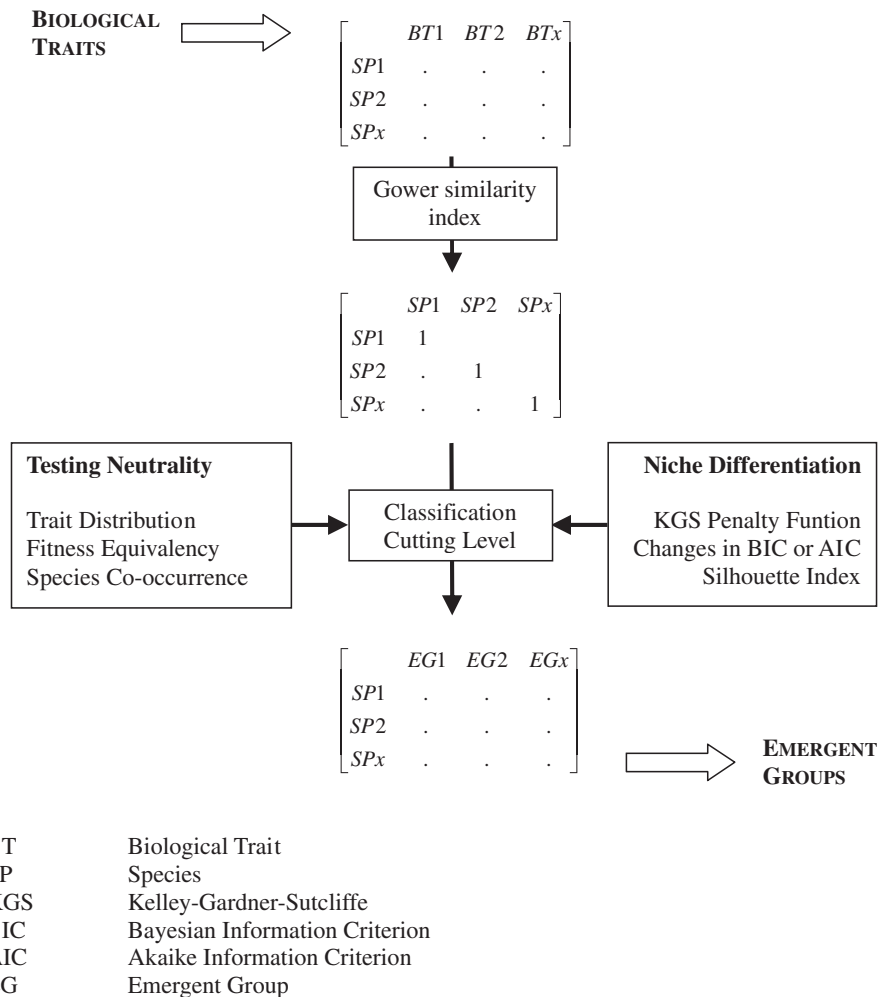


Fig. 1. A methodological framework for delineating, maximizing niche differentiation between and testing neutrality within Emergent Groups. See text for details. BT – Biological Trait; SP – Species; KGS – Kelley-Gardner-Sutcliffe; BIC – Bayesian Information Criterion; AIC – Akaike Information Criterion; EG – Emergent Group.

distributions are well-predicted by both neutral and non-neutral models (Chave et al., 2002). We are thus restricted to **test** the basic assumptions underlying the theory:

- (1) At the biological trait level, the distribution of any trait, or trait combination, should exhibit no correlation with species abundances within Emergent Groups because species belonging to a single Emergent Group are assumed to be competitively equivalent. Therefore, even **subtle differences in species traits should not predict the identity of dominant versus rare species** (Harpole and Tilman, 2006).
- (2) At the demographic level, the assumption of equivalence among individuals is difficult to assess *sensu stricto*. However, Chave (2004) suggests (i) to test the equivalence of demographic parameters (recruitment and death rates) among species and (ii) to test the fitness equivalence throughout time using the ratio of birth rate over death rate. However, we must bear in mind that equivalence among species is required but not enough to verify equivalence across individuals (Chave, 2004).
- (3) At the species level, a key test of the neutral theory is how likely species of an Emergent Group are to co-occur in a given biogeographical area. Indeed, if particular species tend to occur together, it would suggest that some additional environmental variables shape the Emergent Group composition. The simplest way of investigating the tendency of species to occur together is the measure of correlation between all pairwise combinations of species. If Emergent Groups were not successfully defined, there will be more highly positive and highly negative correlations than would be expected by chance (Bell, 2001).

Functional redundancy and functional divergence

Central to the Emergent Group approach is the assumption of functional equivalence within Emergent Groups. This is implicitly assumed by many community ecologists when aggregating species into functional groups, trophic levels or with respect to any biological traits (e.g. body mass, lifespan, etc.). The idea of functional equivalence is closely linked to the concept of functional redundancy (Naeem, 1998; Rosenfeld, 2002; Walker, 1992). Redundant species are defined as species performing the same functional role in ecosystems so that changes in species diversity do not affect ecosystem functioning (Loreau, 2004). The ‘functional group’ literature is remarkably silent about the assumption of equivalence and redundancy (Hubbell, 2005) and there have been relatively few theoretical efforts to question their commonness in natural systems (Loreau, 2004). If some species (members of an Emergent Group) behave like functional redundants, both their local fitness and their fitness changes across environmental gradients are similar (Leibold and McPeck, 2006). The biotic and abiotic environment will thus regulate the total abundance of all redundants and not the abundance of each individual species. Therefore, the Emergent Group richness in a local community is subject to a zero-sum rule set by the balance between the rate of individual loss and the rate of immigration (of an individual from the same Emergent Group) from the metacommunity. Redundant species are thus guarantors of reliable ecosystem functioning (Naeem, 1998). Indeed, local extinction of an individual will be followed by a compensatory arrival, which effectively leads to a replacement of the contributions of the lost individual to overall system functioning.

Also central to the Emergent Group approach is the assumption of functional divergence between Emergent Groups. Emergent Groups diverge in terms of functional (physiological, morphological, phonological, etc.) processes related to specific biological traits, i.e. the functional or theoretical niche, and in terms of responses to environmental factors that will mediate how the functional processes can be performed, i.e. the ecological or realized niche (McGill et al., 2006a). In this way, tradeoffs such as seed size/seedling competitiveness, investment in reproductive system/investment in vegetative system or competitive ability/predator invulnerability (for a review, see Kneitel and Chase, 2004) are cornerstones of the divergence between Emergent Groups. Recognizing niche differentiation between Emergent Groups provides interesting means to overcome the main limitation of neutral theories: to predict ecosystem responses to environmental changes (Chase, 2005). For example, neutral theories fail to reproduce the rapid landscape-level changes in species composition

apparent in plant communities from many semi-arid areas because the only mathematical term that can link dynamics among local communities is dispersal (Adler, 2004). Incorporating deterministic elements shaping the distribution of biological traits can help to predict these abrupt changes in floristic composition in semi-arid areas (Hérault and Hiernaux, 2004). Furthermore, use of the Emergent Group framework allows differentiation of Emergent Groups according to their dispersal abilities. This is interesting because species with poor dispersal abilities are influenced by neutrality at small scales whereas highly dispersed species should be at larger scales (Thompson and Townsend, 2006). Emergent Groups with low rates of dispersal have species that should be very aggregated while the most abundant species belonging to Emergent Group with very high rates of dispersal should be present almost everywhere. This is an interesting way to assess the coexistence of matrix and patchy Emergent Groups in a given local community (Hérault and Honnay, 2005).

Thus, the Emergent Group approach stipulates that neutral communities of functionally equivalent species relate to each other through niche differentiation. In this way, the number of Emergent Groups in a local community could be a measure of functional diversity whereas the number of species per Emergent Group could be a measure of functional redundancy (Alonso et al., 2006). On one hand, the functional diversity is a greater determinant of ecosystem processes than the species richness itself (Tilman et al., 1997). On the other hand, the functional redundancy is a greater determinant of ecosystem stability than the species richness itself (Naeem, 1998). This approach may thus pave the way to resolve the endless debates concerning diversity/stability and diversity/ecosystem functioning (Hooper et al., 2005; Loreau et al., 2001).

Concluding remarks

The main challenge is now to determine empirically which group of organisms behave neutrally by applying the following framework: (i) subdividing the species of a given metacommunity on the basis of their biological traits, (ii) examining interactions among species in each Emergent Group and testing neutrality and (iii) examining how changes in Emergent Group abundances affect ecosystem processes and vice versa. First, we need to acknowledge that it is extremely unlikely that we can measure a large array of biological traits for an entire regional pool of species. Therefore, we need to search for synthetic traits that are easy to measure and of great relevance. For example, seed mass can be used as a synthetic trait that simultaneously captures various aspects of dispersal (seed longevity,

dispersal distance) and establishment success (Lavorel and Garnier, 2002). Another stumbling block is: How can the real existence of Emergent Groups be experimentally tested? I believe that experimental additions or removals that measure intra-Emergent Group abundance responses will provide a very sensitive test (Díaz et al., 2003). If the Emergent Group hypothesis is valid, the Emergent Group should numerically compensate to maintain a similar level of abundance, all else being equal. In this way, there is a fixed contribution (defined by the functional niche) of the Emergent Group to the local community. This can also be demonstrated by an unusually low variation in the abundance of each Emergent Group throughout time indicating that, within a given Emergent Group, individuals replacing lost individuals are not a random subset of the regional pool of species (Bossuyt et al., 2005).

Many researchers agree that neutral and niche-differentiation processes probably operate simultaneously to generate and maintain diversity in ecological communities (e.g. Brokaw and Busing, 2000; Palmer, 2001). In fact, Hubbell (2001) expects a future unification of the neutral and niche theories. New models incorporating both stochastic 'neutral' and deterministic 'niche-based' processes are already beginning to appear (e.g. Tilman, 2004). Indeed, most ecologists feel that niche theories *sensu stricto* are inadequate because the number of species is greater than the number of niches and that neutral theories *sensu stricto* are inadequate because the number of equivalent species is less than the number of trophically similar species. The Emergent Group approach proposes that neutral and niche theories are two theoretical frameworks working at different integration levels: neutrality among individuals of an Emergent Group and niche differentiation among Emergent Groups of a local community. This approach is dependent on the assumption that, within a given Emergent Group, species are functionally equivalent to each other in most important aspects. Therefore, I largely endorse the opinion of Scheffer and van Nes (2006), who stated that there are two alternative ways to survive together: being sufficiently different or being sufficiently similar.

Of course, the Emergent Group concept has mostly emerged from theoretical studies and by now this has to be tested. Anyway, the way in which niche and neutral models could be combined provides an opportunity for theoretical scientists and empirical ecologists to collaborate fruitfully. The recognition that, within a local community, different combination of biological traits (Emergent Groups) have different functional niches, have different dispersal abilities and have different spatial aggregation patterns should make many field ecologists less sceptical about neutral models. Too often in the development of ecology there have been fierce battles between supporters of two extremely divergent

theories (associations *versus* continua, equilibrium *versus* disequilibrium, etc.) with the too-late realization that both approaches were valid (Walker, 1992). In the ensuing debate on how to model biodiversity, I have no doubt that the use of both niche and neutral models will turn out to be relevant, at different integration levels.

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