LETTER

Reconciling niche and neutrality: the continuum hypothesis

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Abstract

In this study, we ask if instead of being fundamentally opposed, niche and neutral theories could simply be located at the extremes of a continuum. First, we present a model of recruitment probabilities that combines both niche and neutral processes. From this model, we predict and test whether the relative importance of niche vs. neutral processes in controlling community dynamics will vary depending on community species richness, niche overlap and dispersal capabilities of species (both local and long distance). Results demonstrate that niche and neutrality form ends of a continuum from competitive to stochastic exclusion. In the absence of immigration, competitive exclusion tends to create a regular spacing of niches. However, immigration prevents the establishment of a limiting similarity. The equilibrium community consists of a set of complementary and redundant species, with their abundance determined, respectively, by the distribution of environmental conditions and the amount of immigration.

INTRODUCTION

The main aim of community ecology is to predict the distribution and abundance of species in space and time. Two distinct families of theoretical models have been developed towards this end. Models of niche differentiation are the basis for the vast majority of coexistence theories and have been used to explain the distribution and abundance of a wide range of taxa in both terrestrial and aquatic environments (see Silvertown 2004 for a review). The second type of model invokes species that are ecologically equivalent and a dynamics governed by stochastic processes of extinction, immigration and speciation (Hubbell 1997, 2001; Bell 2000). The latter models have attracted enormous attention among ecologists because of their surprising simplicity, the apparent accuracy of their predictions for some taxa (Bell 2001; Hubbell 2001; Volkov *et al.* 2003; He 2005) and their highly controversial assumption of species equivalence (Whitfield, 2002; Gaston & Chown 2005). Despite the general agreement that neutral models can predict some aspects of diversity patterns as well or better than previous models (Volkov *et al.* 2003), they have also raised considerable disagreement (Chase 2005). Each type of models has limitations that have been widely discussed

(Chesson 2000; Hubbell 2001, 2005; Chave *et al.* 2002; Chave 2004; Tilman 2004; Chase 2005; Gaston & Chown 2005).

The neutral model is commonly perceived as a null alternative to niche theory (Harte 2004; Gaston & Chown 2005). Tests of the neutral model initially focused on simply comparing empirical patterns of species distribution to the patterns predicted by the model (Bell 2001; Hubbell 2001; Condit *et al.* 2002; McGill 2003a; Volkov *et al.* 2003). This approach has been strongly criticized (McGill 2003b; Nee & Stone 2003; Chave 2004), and subsequent studies have sought to highlight differences in the predictions of the two alternate models and test them simultaneously. Tests of the alternate models have been conducted in a wide variety of ecosystems, including tropical forests (Hubbell *et al.* 1999; Duivenvoorden *et al.* 2002; Potts *et al.* 2002; Tuomisto *et al.* 2003; Hardy & Sonké 2004; Svenning *et al.* 2004; Uriarte *et al.* 2004), temperate forests (Clark & McLachlan 2003; Gilbert & Lechowicz 2004), grasslands (Adler 2004; Fargione *et al.* 2003) and marine ecosystems (Wootton 2005). While some of these tests tended to support either niche or neutral models, in most cases the results were intermediate between the two.

Inconclusive results present a challenge from the strict sense of hypothesis testing. It may be that methodologies or

data sets were not adequate to allow a critical test of the differences between the models. An alternative explanation is that both niche and neutral processes operate in any community. This view appears to be implicitly shared by many ecologists (Hurtt & Pacala 1995; Hubbell 2001; Chase & Leibold 2003; Barot 2004; Gaston & Chown 2005), but has not yet been formally incorporated in models that can explore the relative importance of niche vs. neutral processes.

The processes of the neutral model are birth, death, dispersal and speciation (Hubbell 2001). The model assumes that all species of a community are equal in their traits regarding these processes. As a result, species follow a random walk to extinction (ecological drift). Niche differentiation will impact any of these processes because of distinct relationships with environmental factors (biotic and/or abiotic) and will produce correlations between the species abundance and environment. In this study, we present a simple, unified model of recruitment processes (dispersal and birth) in which both niche and neutral processes are present and where the relative importance of each varies along a continuum. In our model – inspired by Hurtt & Pacala (1995), Hubbell (2001) and Tilman (2004), among others – recruitment is a lottery function of both interspecific differences in competitive ability (niche process) and of local and long distance dispersal limitations (neutral processes). We compare the recruitment probabilities expected for the neutral recruitment model, the niche recruitment model and the unified recruitment model. For simplicity, we assume species are equal in their death probability, although it is obvious that differentiation could also occur through this process. The models also focus on the local community scale. Thus, we do not consider speciation, and we recognize that further work is necessary to unify the models at the metacommunity scale.

Our first objective is to identify the factors – or more specifically the community characteristics – that will determine where on this continuum from niche to neutrality a particular community will lay. Our second objective is then to assess how the distribution of relative abundance of species, and their distribution and organization along environmental gradients, are affected by the relative importance of niche vs. neutral processes. We will first present a simple non-spatial analysis for a two-species community and examine how variation in competitive inequality and local and long distance dispersal are sufficient to create the continuum from niche to neutrality. Then, we extend the analyses to more complex situations with spatially explicit simulations of species-rich communities in a heterogeneous environment.

The first prediction we will test is that the 'neutrality', i.e. the ecological drift of a community increases with species niche overlap. Second, we predict that neutrality increases with species richness, because: (i) increasing richness along a finite environmental gradient implies an increasing species packing along the gradient (and thus potentially a greater fundamental niche overlap); and (ii) an inverse relation between average population size and richness in a community of fixed size (and thus dispersal limitation). Third, we predict a positive relationship between neutrality and dispersal capabilities. Increasing dispersal abilities increase the relative abundance of inferior competitors in the local propagule supply (from source populations elsewhere in more favourable sites in the neighbourhood or the region), and thus decrease the impact of species inequalities. Finally, following Tilman (2004) we expect that in the absence of immigration, diversity will stabilize once a limiting degree of similarity is reached. However, we predict that immigration would counteract the limiting similarity by constantly rescuing rare species from stochastic extinction, thus increasing the neutrality of the local community.

MODEL DESCRIPTION

Recruitment under neutral and niche processes

Recruitment of new adults in our model follows the lottery process of Hubbell's neutral model (Hubbell 1997, 2001), to which we add niche differentiation in a spatially heterogeneous environment. Recruitment events only take place following the death of an adult, because of intense competition for space. At each time step, a certain fraction of adults dies at random and is replaced by recruits originating from either the local community or by immigration from the metacommunity. The probability that an adult will be replaced by a particular species in Hubbell's neutral model is given by the species' relative abundance at both local and regional scales (i.e. the metacommunity):

$$R_i = (1 - m)\left(\frac{N_i}{J}\right) + m(P_i), \qquad (1)$$

where parameter m is the probability that a recruit is an immigrant coming from the metacommunity. The first term is the contribution of the local population of species i to the propagule supply, given by its abundance N_i over the size J of the local community. The second term is the contribution of the metapopulation of species i to the propagule supply, given by its relative abundance P_i in the metacommunity.

Hubbell's neutral model is spatially implicit because it distinguishes the local community and the metacommunity. This poses the problem of defining the boundaries of the local community and assuming uniform dispersal within this community. The model can be made more spatially explicit by recasting it in terms of dispersal processes. At a given replacement site, the composition of the propagule supply is the result of the dispersal from parents, regardless of

whether they are 'local' or 'regional' individuals. A spatially explicit but neutral model of recruitment then takes the form:

$$R_i = \frac{\sum_{r=1}^{n} N_{i,r} W(r)}{\sum_{j=1}^{s} \sum_{r=1}^{n} N_{j,r} W(r)}, \qquad (2)$$

where the recruitment probability of species i is the sum of its propagules coming from N conspecific adults located at all r distances, weighted by the dispersal function $W(r)$, divided by the sum of the propagules coming from adults of all j species at all r distances. Modelling the recruitment probability with a local dispersal kernel avoids the need to define boundaries for the local community because each replacement site has its own neighbourhood. However, it could include immigration from a metacommunity. A typical dispersal kernel is usually a steeply decreasing function of distance, but with a long 'fat' tail (Nathan & Muller-Landau 2000). The area under the remote part of the tail corresponds conceptually to the contribution of the meta-community to the propagule supply through long distance dispersal (i.e. immigrants). Therefore, immigration can be modelled with a continuous kernel when one has an exact image of the metacommunity and the fat tail of the kernel; otherwise it can be approximated by modelling a quantity of immigrants in the propagule supply with a constant based on the relative abundance of each species in the metacommunity.

We introduce niche differentiation during the replacement process by considering that propagules have to survive in the understorey of adults prior to recruitment to adult size. Survival probability (λ_i) is a species-specific function of an environmental factor E (using a Gaussian function, such as in Tilman 2004 – see Fig. 1):

$$\lambda_i(E) = \exp\left[\frac{-(E - \mu_i)^2}{2\sigma^2}\right], \qquad (3)$$

where μ_i represents the optimal environmental condition for species i and σ is a parameter defining fundamental niche breadth. In this simple model (and ignoring dispersal limitation), the probability that a recruit will be of species i in a given environment is:

$$R_i = \frac{\lambda_i}{\sum_{j=1}^{s} \lambda_j}. \qquad (4)$$

In such a model, species inequality varies as a function of niche overlap (schematically illustrated in Fig. 1).

When we combine these neutral and niche processes, the recruitment probability of species i at a given site is a function of the composition of the propagule supply at the replacement site and the specific survival rates (assuming independence of dispersal and survival). Then, with species equal for all traits except for survival as a function of E, the
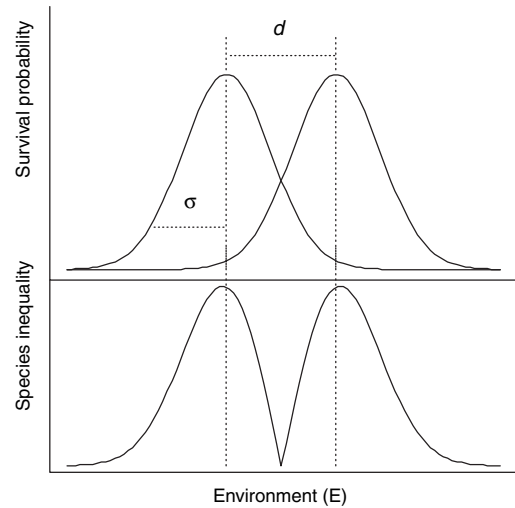

Figure 1 Schematic illustration of species fundamental differentiation along an environmental factor E. The fundamental niche overlap is inversely related to the distance between adjacent niches d divided by the fundamental niche breadth σ. The species competitive inequality is given by the difference of survival probabilities between species at each value of the gradient E. Species are ecologically equivalent at a value of E where inequality is nil and their inequality increases with the distance for this 'neutral' point. Species inequality declines with a decline in d or an increase in σ.

probability R_i of species i being recruited in a replacement event is:

$$R_i = \frac{\sum_{r=1}^{n} \lambda_i N_{i,r} W(r)}{\sum_{j=1}^{s} \sum_{r=1}^{n} \lambda_j N_{j,r} W(r)}. \qquad (5)$$

Equation 5 is a simple form of a spatially explicit recruitment model that takes into account both niche differentiation and neutral processes. Here, niche differentiation is based on interspecific differences in juvenile survival as a function of a single environmental axis (eqn 4). However, it could also have been based on differences in terms of growth, fecundity or germination, or even more complex mechanisms such as interactions with other trophic levels like animal dispersal in particular environmental patches, pest, herbivory and predation resistance. The neutral process in this model is dispersal limitation (eqn 2), because of the spatial distribution of the different populations of a community and their respective dispersal.

Before presenting the spatially explicit simulations, we will first use three examples, based on the simple model described above, to illustrate how the relative importance of niche and neutral processes in eqn 5 can vary depending on competitive inequality (eqn 4) and species relative abundance in the propagule supply (eqn 2). These examples are necessary to explain the predictions further tested by

simulations. The figures show the recruitment probability of a focal species in a two species competition during a single recruitment event, calculated from eqn 5. In all three examples, we assumed the environment (E) at the recruitment site to be homogeneous and the two species to be equal in all traits except for their optima (μ) (detailed parameters are given in the legend of Fig. 2).

The first example (Fig. 2a) illustrates a transition from stochastic to competitive exclusion as a function of species similarity. The figure depicts the recruitment probability of two species at equal abundances in the propagule supply, as a function of the distance between their niche optima. The upper line corresponds to the species at its niche optimum and the lower line to the inferior competitor. The dashed line corresponds to the recruitment probability under a neutral model. The difference between the recruitment probabilities increases with the distance between the niches. Systematic competitive exclusion will be achieved with species having sufficient differences in their recruitment probabilities, as in the classical competition trials pioneered by Gause (1934) demonstrating competitive exclusion. However, according to the neutral model, further trials with equivalent species would have lead to a stochastic exclusion through a 'random walk to extinction'. As a consequence, the exclusion will be more deterministic as species differentiation increases.

In the second example (Fig. 2b), we show that extreme dispersal limitation can counteract competitive inequalities. In this example, the focal species is represented by a single propagule (invasion event) among a total input of 100 propagules, and has an optimum (μ) that corresponds to the prevailing environmental condition (E). A minimum distance between the niche optima of the invader and resident species is necessary to counteract the resident species' advantage conferred by its higher relative abundance. This minimum distance varies depending on niche breadth. Without dispersal limitation, we would expect competitive exclusion to result in the species with the highest survival to exclude the other. However, the resident species has many more propagules than the invader, and thus has a demographic advantage even if it has lower survival. The more similar the two species are, the closer the recruitment probability is to the one of a neutral model (dashed line).

Finally, the third example (Fig. 2c) shows that variation in the relative abundance of species interacts with competitive inequalities to determine the recruitment probability. In this example, the focal species is the inferior competitor and its recruitment probability is given as a function of its relative abundance in the propagule supply. The neutral prediction is shown by the dashed line and the niche prediction without dispersal limitation is illustrated by the horizontal dotted line. Our continuum model (solid line) predicts the
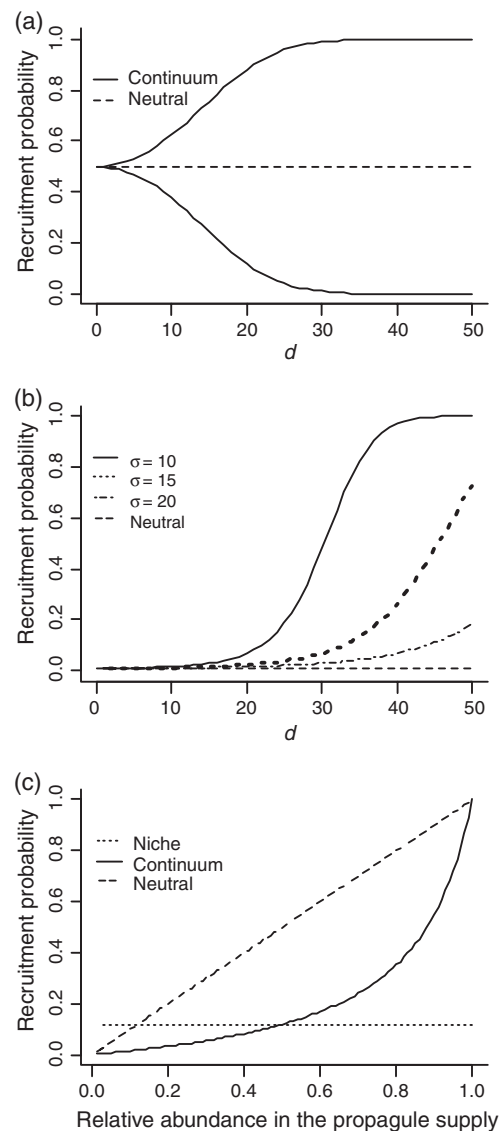

Figure 2 Variation in recruitment probabilities for a two species community, following eqn 5. The environment in the replacement cell is fixed at a value of $E = 50$. (a) The recruitment probabilities of two species with equal abundance in the propagule supply. The superior and the inferior competitors are the upper and lower solid lines respectively. The dash line is the neutral prediction. $\sigma = 10$, $\mu_1 = 50$, $\mu_2 = 50 -$ distance between niches. (b) The recruitment probability of a superior competitor arriving as a singleton in the community increases as a function of distance between the niches, for different niche breadths. The dash line is the neutral model considering a community size of 100 individuals. $\mu_1 = 50$, $\mu_2 = 50 -$ distance between niches. (c) The recruitment probability of an inferior competitor as a function of its relative abundance in the propagule supply. The dotted line is predicted by the pure niche model of eqn 4. The dash line is the neutral prediction. $\sigma = 10$, $\mu_1 = 30$, $\mu_2 = 50$.

recruitment probability of an inferior competitor to be lower than that predicted by a pure niche model, until the inferior competitor reaches a relative abundance of 0.5. After that threshold, the recruitment probability under the model combining niche differentiation and dispersal limitation is higher than the prediction under niche differentiation alone. Eventually, the inferior competitor reaches equal and even higher recruitment probabilities than the superior competitor.

Multispecies spatially explicit simulations

It is not possible to extend the simple analytical model presented above to multispecies communities and a spatially explicit environment. Therefore the following analyses rely on simulations. We used SORTIE-ND (http://www.sortie-nd.org), an open-source software platform for spatially explicit simulation of forest dynamics to implement our model. Two life stages are considered in the model: adults and juveniles. The only processes included in the model are: (i) adult mortality; (ii) dispersal; (iii) species-specific differences in juvenile survival as a function of environmental conditions; and (iv) recruitment from the juvenile to adult stage. The community is represented by a grid of 10 000 adults and is modelled as a torus to avoid edge effects. Each cell of the community grid can be occupied by only one adult. This grid is superimposed on a coarser scale grid that specifies environmental values for each adult cell: each cell of the environment grid is 5×5 adult cells in size. For simplicity, the environment is reduced to a single factor E, with conditions in each cell of the environment grid drawn randomly from a uniform distribution that ranges from 0 to 100. We assumed a uniform distribution to assure each species has the same probability of finding its optimal environment, and thus equivalent dispersal limitation. Unless otherwise noted, all runs use the same grid of environmental values.

At each time step, the model executes the routine summarized in Table 1. First, a fraction of the adult

Table 1 Summary of the model simulation routine and corresponding parameters

Step	Event	Parameters
1	Adult random mortality	Mortality rate (non-specific)
2	Dispersal	Dispersal w (non-specific)
		Immigration m (specific)
3	Juvenile survival	Niche mode μ (specific)
		Fundamental niche breadth σ (non-specific)
		Grid of E values (independent of species occurrence)
4	Juvenile recruitment	–

community is killed at random. All adult individuals are equal in their probability of death. We fixed the adult mortality rate at 25% per time step, comparable with values used in similar models (see Chave *et al.* 2002; McGill 2003a). The mortality rate would not be expected to affect the predictions of a niche model unless species are differentiated by, for instance, lifespan and/or their responses to disturbance regimes (Loehle 2000).

The second step consists of the dispersal of juveniles by residual adults. Unfortunately, because computation time increases rapidly with the size of the community, we could not simulate an entire metacommunity. Instead, we simulated local community dynamics with a simplified treatment of dispersal from the surrounding metacommunity, as in previous neutral models (Bell 2000; Hubbell 2001; Chave *et al.* 2002). Dispersal within the simulated community was modelled with a continuous dispersal kernel as suggested above. The probability of a juvenile reaching a cell located at a distance r from an adult parent of the local community is modelled with the following kernel:

$$W(r) = e^{-wr^2}, \tag{6}$$

where w determines the shape of the dispersal kernel. The value of w was chosen to produce a default median dispersal distance of five adult cells, which by analogy is *c.* 25 m in a forest with trees of 5 m crown diameter. The parameter m in eqn 1 gives the proportion of juveniles from all species that reached the local community via non-spatially explicit immigration. The metacommunity was assumed to be constant in composition and species relative abundance was assumed to follow a log-series distribution. Preliminary trials showed the results to be the same with a uniform distribution of species in the metacommunity. Bell (2000) assumed a stationary uniform distribution of species abundances in the regional species pool and found results consistent with Hubbell (2001). Thus, each species has a probability of immigration scaled to its abundance in the metacommunity. Fecundity is equal for all species and was determined from preliminary trials so that the combined input from local and long distance sources would produce *c.* 10–20 juveniles per adult. By comparison, this corresponds roughly to sapling density in temperate forests (Pacala *et al.* 1996). Results from preliminary simulations were not sensitive to fecundity, and therefore we do not discuss it further.

Niche differentiation occurs in the third step (Table 1) through variation among species in juvenile survival as a function of the environmental condition within the grid cell (eqn 3; Fig. 1). Each species has a unique niche optimum (μ_i), and the niches are regularly spaced along the environmental axis. The distance between adjacent niche optima corresponds to the range of E (100) divided by the number of species. Unless otherwise specified,

niche breadth (σ) was set at 10 and was equal for all species.

Finally, when an adult dies, it is replaced by a juvenile picked at random from those located in the adult cell. Juveniles stay in the understorey of adults until they are recruited or die. Thus, the recruitment probability for species *i* in a given adult cell is equal to the relative abundance of that species among the juveniles in the cell. Preliminary testing confirmed that this model produces competitive exclusion when niche differences are sufficient, while it creates a random drift when species are ecologically equivalent.

Simulation scenarios and data analysis

The first set of simulations was a gradient of species richness from 5 to 100 species. Two different scenarios were used. In the first, a constant niche overlap (i.e. distance between niches/niche breadth = 1) was maintained as species richness increased through a decrease in niche breadth. This allowed us to test the effect of increasing dispersal limitation with increasing species richness, without the effect of increasing niche overlap. In the second scenario, we held niche breadth constant ($\sigma = 10$) to test the effect of increasing niche overlap with increasing species richness.

The second set of simulations tests the consequences of increasing niche overlap (through an increase in niche breadth from 1 to 50) in a community of 10 species. The third set of simulations tests the consequences of increasing dispersal capabilities. We varied the dispersal parameter *w* to produce a gradient of median dispersal distance from 5 to 50 m in a community of 10 species. The above simulations did not include immigration to track the neutral drift. For these simulations, all runs start with 25 saplings of each species per adult cell. By doing so, a fast selection of the top competitor occurred for each site at the beginning of the run and thus prevents dispersal limitation at the initiation of the simulation.

A community solely driven by competition will have a deterministic succession, while a neutral community will have the maximum stochasticity among replicated successions because of the neutral drift (Clark & McLachlan 2003). We used this proxy to assess 'neutrality' when we tested the different predictions presented above. For each of the three sets of simulations described above, we repeated the simulations with all species having the same niche optimum. This serves as a 'neutral control'. We then calculated a 'neutrality index' by dividing the variance in species abundance among replicated runs under a given scenario (differentiated species) by the variance among replicates for the 'neutral control' (undifferentiated species). The index ranges from 0 to 1, with 0 being absolutely deterministic (niche) and 1 being completely stochastic (neutral). The

variance was calculated for each species among 50 replicated runs and then averaged for the whole community. The index was calculated after 500 time steps. This is not a sufficient run length to reach a truly stable species composition, but preliminary simulations showed that index differences among scenarios were similar when the run length was longer than 500 time steps.

We compared the abundance distribution of species with different levels of immigration. We simulated communities in which none, 10^{-3} and 10^{-1} of the new juveniles each time step were immigrants. The metacommunity consisted of 149 differentiated species with their optima drawn at random (distance between niches = 0.67, and niche breadth $\sigma = 10$). Simulations were run until composition stabilized (5000 and 20 000 time steps, respectively, with and without immigration). Species arrive in an initially bare community following immigration events, except for the scenario without immigration where we started the community with the set of 149 species. For comparison with Tilman (2004), a scenario with a fraction of 10^{-1} immigrants and a Gaussian frequency distribution of environmental conditions was also simulated. Species were ordered by their niche optimum and their abundance plotted to visually examine the abundance against the distance between niches for the different scenarios.

SIMULATION RESULTS

Species richness and niche overlap

Increasing species richness resulted in increasing neutrality, whether niche overlap was kept constant or increased (Fig. 3a). Increasing species richness increases the potential for dispersal limitation (i.e. lack of propagules to colonize suitable sites) and thus promotes neutrality. We did not observe a pattern of 'realized partitioning' in the high species richness scenarios (Tilman 2004; Schwilk & Ackerly 2005). In principle, species could have colonized the most favourable sites, reduced their realized niche breadth and maintained their dominance on these sites, but we did not observe this in the simulations. There was also a clear relationship between niche breadth and neutrality in the set of simulations with increasing species fundamental niche breadth (Fig. 3b). In those simulations, dispersal limitation was low and constant among scenarios. Again a realized partitioning of the environment could have occurred despite increasing fundamental niche breadth, but it was not observed in the simulations.

Local dispersal

Neutrality increased as local dispersal distances increased, as predicted (Fig. 3c). However, the effect was much less pronounced than what was observed when species richness
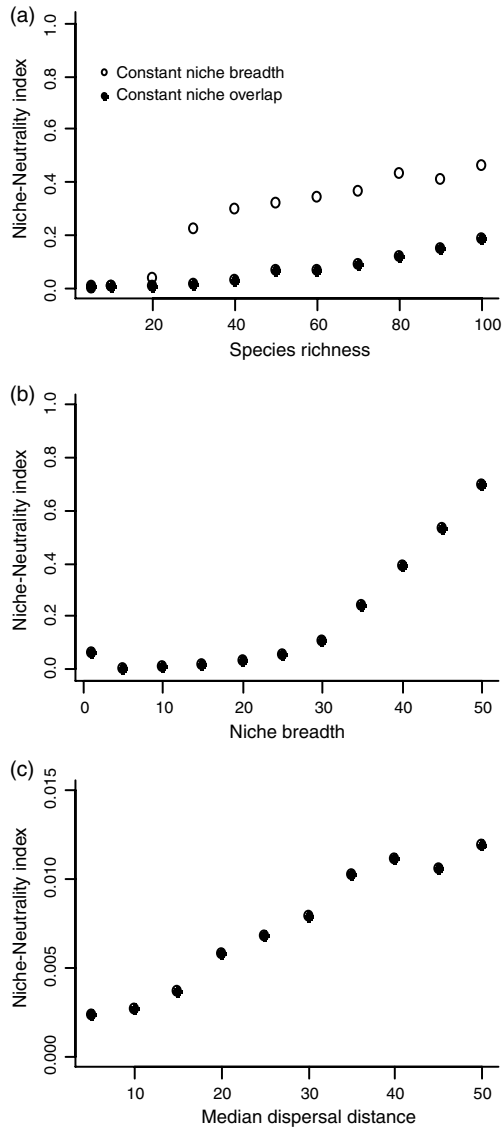
Figure 3 Gradient from niche to neutrality as a function of: (a) species richness with constant niche breadth ($\sigma = 10$) and constant niche overlap ($d/\sigma = 1$); (b) niche breadth; (c) median dispersal gradient. Environmental values E ranges from 0 to 100, each species has a unique niche and a cell of the environmental grid is 5×5 adults in size. Unless specified by the scenario, default niche breadth $\sigma = 10$, median dispersal distance = 5 adults, species richness = 10 species. There is no immigration in these simulations. The index ranges between 0 (niche) and 1 (neutral).

and niche overlap were increased (Fig. 3a,b). It is possible that the range of the stochasticity gradient could have been affected by the arbitrary choice of the grain size of the environment. For these simulations, the environment was simulated as a grid of cells holding 25 adults. We performed simulations with different grain sizes (not shown) and found that neutrality is inversely related to grain size. Under the

assumption of spatial heterogeneity fixed in time, the likelihood that a propagule falling from an adult already located on a favourable site lands on a favourable site depends on the dispersal capabilities relative to the grain size of the environment. Thus, the capacity of a superior competitor to maintain its occupancy of a suitable site, against successful stochastic recruitment of inferior competitors, is inversely related to the ratio of the dispersal capabilities over the grain size.

Immigration

Simulation with no immigration (i.e. local dispersal only) produced communities of low diversity (13 species of a regional pool of 149), and regular spacing between the dominant species' niche optima (i.e. clear limiting similarities) (Fig. 4a). Increasing amounts of immigration resulted in increasing numbers of rare species in the community (Fig. 4b,c), as predicted by neutral models (Bell 2000; Hubbell 2001). At a low immigration level (Fig. 4b, 43 species), the rare species were located between the dominant species, which were still more or less regularly spaced. Thus, at low immigration rates, the pattern of relative abundance of species within a community will be strongly influenced by the distribution of environmental conditions. The specific identity of the winners in the successional contest will be the result of the sequence of invasion events at the beginning of the succession, since the first species to arrive at a site can limit the success of the subsequent immigrants by stochastic exclusion (Tilman 2004). As the amount of immigration increases, the community structure will be increasingly affected by stochastic exclusion (Fig. 4c, 149 species). At high immigration rates, there will be a high degree of niche overlap and similar species will be subject to neutral dynamics.

The last simulations revealed an important interaction between environmental heterogeneity and immigration (Fig. 4d). A change in the frequency distribution of the environmental conditions can have a considerable impact on the relative abundance distribution of species, even with a relatively high amount of immigration. Under the assumption of a Gaussian frequency distribution of environmental conditions (Fig. 4d), the frequency of rare species is considerably higher than under a uniform distribution of environmental conditions (Fig. 4c). These rare species are more dispersal limited and thus subject to drift, but they are sustained by immigration (under a form of source–sink dynamics) and successfully reintroduced after local extinction.

DISCUSSION

Our analyses suggest three general conclusions. First, competition and stochastic exclusion can both simulta-
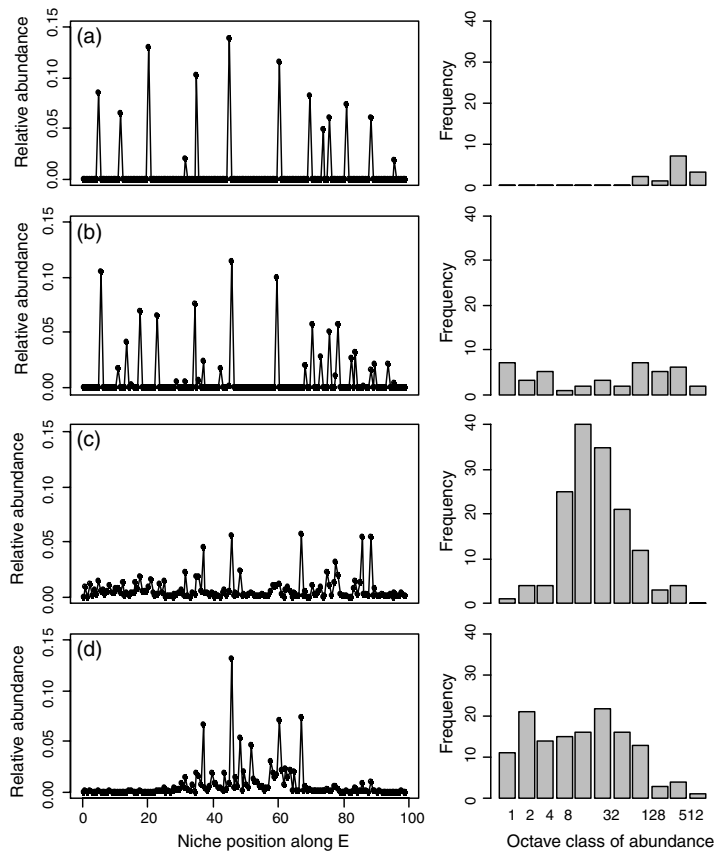
Figure 4 Species abundance distributions at different immigration intensities: (a) $m = 0$; (b) $m = 0.001$; (c) $m = 0.10$; (d) $m = 0.10$, but the distribution of environmental values E follows a Gaussian distribution. On the left side of the figure, the species are ordered by the rank of their niche optimum along the gradient of E. On the right side are the corresponding frequency distributions of species abundance by octave class of abundance (sensu Preston 1948). Default parameters are the same as in Fig. 3.

neously drive community dynamics and structure species assemblage. The relative importance of competitive vs. stochastic exclusion creates a continuum from niche-structured communities to neutral structure. Second, joint effects of competition and dispersal are sufficient to create this continuum. Competitive inequality between species determines the extent to which demographic limitations in the propagule supply will affect community dynamics. In turn, demographic limitations are created by the interplay of the spatial configuration of the community with the dispersal capabilities at both local and long distance. Ultimately, the pattern of relative abundance of species within a community results from the balance between competitive and stochastic exclusion. In relatively isolated communities, immigration from metacommunities is insufficient to balance the exclusion processes, diversity is low, and niche differentiation is ultimately the dominant process affecting species abundances. The species tend to have non-overlapping niches, and their relative abundance depends on the distribution of environmental conditions. Rare species will be maintained with increasing immigration. Thus, high immigration prevents the establishment of a limit to similarity and increases species richness. In such conditions, niche overlap is high and community dynamics is dominated by stochastic exclusion.

Numerous studies have incorporated stochasticity in models of recruitment, following the work of Hurtt & Pacala (1995). Among them, Tilman (2004) has proposed a stochastic niche theory as a revision of classical competition theory (Tilman 1982). The stochastic niche theory predicts patterns of species relative abundance that are similar to those predicted by the neutral model. In Tilman's (2004) model, the structure of abundance of a community results from the interplay of the frequency distribution of environmental conditions and specific traits of the invaders (Tilman 2004). The establishment of a stochastic limit to similarity prevents infinite diversity. Thus, the diversity of a community under this model depends on the capacities of the species to partition the environmental gradient. However, Tilman (2004) did not take into account the impact that various intensities of immigration and dispersal limitation could have on the predicted outcome. The results presented here clearly demonstrated that these are factors that can counterbalance niche differentiation. Therefore, we argue the stochastic niche theory is not a complete reconciliation between niche and neutrality.

Under neutral models, the shape of the relative abundance distribution results from the balance between stochastic exclusion and the supply of new species (Bell 2000; Hubbell 2001). Some models that also include niche

differentiation (Chave *et al.* 2002; Purves & Pacala 2005) can produce similar relative abundance patterns, as long as species richness is kept elevated through substantial immigration or speciation. It has been argued that observing patterns of species abundance typically predicted by neutral models cannot necessarily be taken as evidence of neutral processes (Purves & Pacala 2005), and our results concur with that. However, our results also show that the observed patterns can result from a neutral drift created by an elevated niche overlap, sustained by the constant reintroduction of excluded species through high immigration and/or speciation rates. Under such conditions, the rare species are transients and their occurrence depends on immigration; on the other hand, the resident species are permanent and their occurrence depends on niche differentiation (Magurran & Henderson 2003; Schwilk & Ackerly 2005).

A model of community dynamics that unifies recent theoretical developments to predict patterns of species abundance should combine the dispersal limitation component of the neutral models and the stochastic niche concept pioneered by Tilman (2004). The model we proposed incorporates these two concepts in a manner that unifies these perspectives. According to our model, diversity patterns are the consequence of the balance between stochastic and competitive exclusion. In the absence of immigration and speciation, species differentiation tends to create a regular spacing of niches along an environmental gradient, as would be predicted by the stochastic niche model of Tilman (2004). These species are complementary because they do not compete intensively with each other. Their abundance is dictated by the frequency distribution of environmental conditions. Between these complementary species, immigration and speciation will introduce to the community species that are similar to the complementary species. Because these species are redundant to some of the resident species, they will tend to be excluded both by competition and random drift. By chance, in some rare events, they could replace the dominant species after a random drift. The importance of immigration will determine the amount of redundancy, and as a consequence, the balance between stochastic and competitive exclusion in structuring communities. Ultimately, we expect the species richness and diversity structure of a community to be a function of the frequency distribution of environmental conditions, community isolation (because of dispersal limitation, species turnover rate and spatial distribution of resources) and speciation processes (in intensity and diversity of species traits).

CONCLUSION

One of the most important innovations of neutral models has been to explicitly link local community dynamics to metacommunity dynamics. In this study, we used a simplified representation of this interaction by assuming that the distribution of species relative abundance in the metacommunity corresponded to a stationary log-series. Essentially, we incorporated the metacommunity using a mass-effect perspective (Leibold *et al.* 2004), where the metacommunity is a source of immigrants that can potentially rescue extinct species and introduce new species in the local community. However, in reality, metacommunities are obviously dynamic. Under the neutral model, speciation is a necessary process to balance the extinction of species at the regional scale (Hubbell 2001). Speciation also creates innovation in species traits, which can impact community dynamics under a niche perspective (Tilman 2004). Combined with dispersal limitation, speciation is responsible for spatial patterns in species distribution. The mass-effect is possible when such regional spatial patterns occur (Mouquet & Loreau 2002). Thus, we agree that local dynamics can be affected by the speciation process at the regional scale. For instance, a non-stationary metacommunity could introduce a greater amount of variability in the identity of the redundant species, and occasionally replace the complementary species. However, we do not expect that a dynamic metacommunity would change the essence of our results, as the mass-effect perspective of the metacommunity would still remain. Nonetheless, we recognize more work is needed to assess the generality of the continuum hypothesis at the scale of the metacommunity.

Perhaps one of the most interesting results of our model is increasing neutrality with increasing species richness. Careful attention must be paid to this prediction. We emphasize that the mechanism generating this prediction is the presumption of increasing niche overlap with increasing species richness. However, we could expect some communities to be species rich and niche dominated, because of a highly heterogeneous environment that enables low niche overlap, just as we could expect some species-poor communities to be neutral because of a homogeneous environment that increases niche overlap. In general, our prediction is that ecological drift will increase with species richness once a community becomes saturated with complementary species and immigration maintains the presence of redundant species.

There is considerable indirect empirical support in the literature for the continuum hypothesis we have presented here. We have argued that the interaction between niche overlap and dispersal limitation is an essential feature for the continuum from niche to neutrality. As Hubbell (2001) has pointed out, the contrast between temperate and tropical forests dynamics offers a clear example of this continuum. There is a well known trade-off between high-light growth and low-light survivorship in temperate forests (Kobe *et al.* 1995). Shade tolerance is thus a successful predictor of

species abundance ranking along a successional sequence (Pacala *et al.* 1996). The predictability of species ranking is much less clear for tropical forests, where important overlap occurs along this trade-off axis (Hubbell 2001), and where species composition in gaps is more reflective of neighbourhood composition (Hubbell *et al.* 1999). However, more direct support for the hypothesis is clearly needed. Among others, one prediction made in our study was that the ecological drift in a succession increases with increasing niche overlap, and thus presumably with species diversity. One could test this by measuring the variability in succession of a two-factor experiment controlling simultaneously for species richness and immigration (e.g. in grasslands). The long-term monitoring of diversity/ecosystem functioning experiments such as BIODEPTH (Loreau & Hector 2001) thus offer a great opportunity for testing one of the main prediction presented here.

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REFERENCES

Adler, P.B. (2004). Neutral models fail to reproduce observed species-area and species-time relationships in Kansas grasslands. *Ecology*, 85, 1265–1272.

Barot, S. (2004). Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos*, 106, 185–192.

Bell, G. (2000). The distribution of abundance in neutral communities. *Am. Nat.*, 155, 606–617.

Bell, G. (2001). Neutral macroecology. *Science*, 293, 2413–2418.

Chase, J.M. (2005). Towards a really unified theory for metacommunities. *Funct. Ecol.*, 19, 182–186.

Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. Chicago University Press, Chicago, IL.

Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.

Chave, J., Mueller-Landau, H.C. & Levin, S.A. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.*, 159, 1–23.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Clark, J.S. & McLachlan, J.S. (2003). Stability of forest biodiversity. *Nature*, 423, 635–638.

Condit, R., Pitman, N., Leigh, E.G. Jr, Chave, J., Terborgh, J., Foster, R.B. *et al.* (2002). Beta-diversity in tropical forest trees. *Science*, 295, 666–669.

Duivenvoorden, J.F., Svenning, J.-C. & Wright, S.J. (2002). Beta diversity in tropical forests. *Science*, 295, 636–638.

Fargione, J., Brown, C.S. & Tilman, D. (2003). Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl Acad. Sci. USA*, 100, 8916–8920.

Gaston, K.J. & Chown, S.T. (2005). Neutrality and the niche. *Funct. Ecol.*, 19, 1–6.

Gause, G.F. (1934). *The Struggle for Existence*. Williams and Wilkins, Baltimore, MD.

Gilbert, B. & Lechowicz, M.J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. *Proc. Natl Acad. Sci. USA*, 101, 7651–7656.

Hardy, O.J. & Sonké, B. (2004). Spatial pattern analysis of tree species distribution in a tropical rain forest of Cameroon: assessing the role of limited dispersal and niche differentiation. *For. Ecol. Manage*, 197, 191–202.

Harte, J. (2004). The value of null theories in ecology. *Ecology*, 85, 1792–1794.

He, F. (2005). Deriving a neutral model of species abundance from fundamental mechanisms of population dynamics. *Funct. Ecol.*, 19, 187–193.

Hubbell, S.P. (1997). A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs*, 16(Suppl. 1), S9–S21.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Hubbell, S.P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.*, 19, 166–172.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B. *et al.* (1999). Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, 283, 554–557.

Hurtt, G.C. & Pacala, S.W. (1995). The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *J. Theor. Biol.*, 176, 1–12.

Kobe, R.K., Pacala, S.W., Silander, J.A. & Canham, C.D. (1995). Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.*, 5, 517–532.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F. *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.

Loehle, C. (2000). Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *Am. Nat.*, 156, 14–33.

Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Science*, 412, 72–76.

Magurran, A.E. & Henderson, P.A. (2003). Explaining the excess of rare species in natural species abundance distributions. *Nature*, 422, 714–716.

McGill, B. (2003a). A test of the unified neutral theory of biodiversity. *Nature*, 424, 881–885.

McGill, B.J. (2003b). Strong and weak tests of macroecological theory. *Oikos*, 102, 679–685.

Mouquet, N. & Loreau, M. (2002). Coexistence in metacommunities: the regional similarity. *Am. Nat.*, 159, 420–426.

Nathan, R. & Muller-Landau, H.C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.*, 15, 278–285.

Nee, S. & Stone, G. (2003). The end of the beginning for neutral theory. *Trends Ecol. Evol.*, 18, 433–434.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K. & Ribbens, E. (1996). Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.*, 66, 1–43.

Potts, M.D., Ashton, P.S., Kaufman, L.S. & Plotkin, J.B. (2002). Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology*, 83, 2782–2797.

Preston, F.W. (1948). The commonness and rarity of species. *Ecology*, 29, 254–283.

Purves, D.W. & Pacala, S.W. (2005). Ecological drift in niche structured communities: neutral pattern does not imply neutral processes. In: *Biotic Interactions in the Tropics* (eds Burslem, D., Pinard, M. & Hartley, S.). Cambridge University Press, Cambridge, pp. 107–138.

Schwilk, D.W. & Ackerly, D.D. (2005). Limiting similarity and functional diversity along environmental gradients. *Ecol. Lett.*, 8, 272–281.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends Ecol. Evol.*, 19, 605–611.

Svenning, J.-C., Kinner, D.A., Stallard, R.F., Engelbrecht, B.M.J. & Wright, S.J. (2004). Ecological determinism in plant community structure across a tropical forest landscape. *Ecology*, 85, 2526–2538.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl Acad. Sci. USA*, 101, 10854–10861.

Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299, 241–244.

Uriarte, M., Condit, R., Canham, C.D. & Hubbell, S.P. (2004). A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter?. *J. Ecol.*, 92, 348–360.

Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424, 1035–1037.

Whitfield, J. (2002). Neutrality versus the niche. *Nature*, 417, 480–481.

Wootton, J.T. (2005). Field parameterization and experimental test of the neutral theory of biodiversity. *Nature*, 433, 309–312.