

IDEA AND
PERSPECTIVE

A niche for neutrality

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Abstract

Ecologists now recognize that controversy over the relative importance of niches and neutrality cannot be resolved by analyzing species abundance patterns. Here, we use classical coexistence theory to reframe the debate in terms of stabilizing mechanisms (niches) and fitness equivalence (neutrality). The neutral model is a special case where stabilizing mechanisms are absent and species have equivalent fitness. Instead of asking whether niches or neutral processes structure communities, we advocate determining the degree to which observed diversity reflects strong stabilizing mechanisms overcoming large fitness differences or weak stabilization operating on species of similar fitness. To answer this question, we propose combining data on per capita growth rates with models to: (i) quantify the strength of stabilizing processes; (ii) quantify fitness inequality and compare it with stabilization; and (iii) manipulate frequency dependence in growth to test the consequences of stabilization and fitness equivalence for coexistence.

Keywords

Coexistence, frequency dependence, neutral theory, niche, plant community, species diversity.

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INTRODUCTION

Much of ecology is built on the assumption that species differ in their niches. Classic studies have shown that species may differ in their use of multiple-limiting resources (Tilman 1982; Grant 1986), their ability to colonize disturbed sites (Grubb 1977), and their response to temporal fluctuations in the environment (Caceres 1997). In theory, niche differences cause species to limit their own populations more than they limit others, promoting coexistence (Chesson 2000). But despite the overwhelming evidence for niche differences (reviewed in Rees *et al.* 2001; Wright 2002), few studies have successfully quantified their importance for maintaining the diversity we observe in natural communities (Silvertown 2004). This gap in the empirical evidence for niche-based coexistence has been highlighted by the recent emergence of a competing explanation for the maintenance of diversity.

Neutral theory (Bell 2000; Hubbell 2001) directly challenges the niche paradigm by proposing that species similarities, not differences, explain the high diversity of many natural communities. Neutral models are built on the

assumption that all species are identical in their fitness and in their effects on one another. The niche mechanisms that ecologists have studied intensively for decades play no role in neutral models, and the only driver of population dynamics is random variation in births, deaths and dispersal. In the absence of speciation, these stochastic events would eventually drive all but one species extinct, but high diversity can occur in neutral communities if extinction rates are slow enough to be balanced by speciation.

Despite their extreme assumptions about species equivalence, neutral models have successfully reproduced fundamental ecological patterns such as species–area relationships and species abundance distributions (SADs) (Bell 2000, 2001; Hubbell 2001). In fact, the SAD predicted by Hubbell's neutral model describes some empirical SADs better than distributions associated with niche theory (Hubbell 2001; McGill 2003a; Volkov *et al.* 2003). Proponents of the neutral model have interpreted these results as evidence that demographic stochasticity and dispersal limitation can be more important than functional differences among species for generating community patterns (Hubbell 2005).

However, more recent work has emphasized the difficulty of identifying underlying processes from patterns like the SAD. Although the fitting of SADs remains controversial, all parties now agree that niche and neutral models can generate very similar patterns (Chave *et al.* 2002; Chave 2004; Bell 2005; Purves & Pacala 2005; Volkov *et al.* 2005). This renders ‘curve fitting’ a weak approach for establishing the relative importance of niche and neutral processes in structuring communities, a fundamental goal of neutral theory (Hubbell 2001; McGill 2003b). Our objective is to offer an alternative framework and empirical approach for reaching this important goal. We focus primarily on plant communities, reflecting our own experience, but our recommendations should apply to any community of ‘trophically similar, sympatric species that actually or potentially compete...for the same or similar resources’ (Hubbell 2001).

In this study, we highlight key axes on which niche and neutral theory make unique, testable predictions by focusing on coexistence – the heart of the debate. We first locate ‘neutrality’ within the framework of Chesson (2000), which treats coexistence as the outcome of both stabilizing mechanisms and fitness inequality. This synthesis of neutral theory with the classical coexistence literature highlights a critical but unexplored question, ‘to what extent does the diversity we observe in natural communities result from strong stabilizing mechanisms (niches) overcoming large fitness differences vs. weak stabilization operating on species of similar fitness (neutrality)?’ Because current analyses of static community patterns cannot answer this question, we outline a series of empirical tests based on population growth rates to quantify stabilizing processes and fitness inequality in nature.

THE CHESON LESSON: CLASSICAL COEXISTENCE THEORY AND NEUTRALITY

Niche and neutral theory are often treated as mutually exclusive explanations for empirical patterns. This false dichotomy obscures the fact that niche and neutral processes simultaneously influence the dynamics of competing species (Bell 2001; Hubbell 2001; Tilman 2004; Gravel *et al.* 2006; Leibold & McPeck 2006; Silvertown *et al.* 2006), and also implies that classical niche theory has ignored the role of species’ similarities in promoting coexistence. In fact, classical theory treats coexistence as the result of both similarities and differences among species. Chesson (2000) formalized this view, showing that the magnitude of niche-based differences necessary to stabilize long-term coexistence depends on how similar species are in average fitness. Neutral models are simply the special case where species have equivalent fitness and there are no stabilizing, niche-based processes.

In Chesson’s framework, niches are called ‘stabilizing processes’ because they buffer the per capita population growth rates of species in a community. Differences among species in limiting resources, climatic tolerances or natural enemies are just a few of many possible examples (Chesson 2000). Stabilizing processes are defined as any mechanism that causes species to limit themselves more than they limit others. Another way of saying this is that niches cause intraspecific effects to be more negative than interspecific effects. As a result, when any one species increases in abundance, its per capita growth rate slows relative to other species, helping to limit competitive exclusion. Thus, a signature of stabilizing processes is that species’ per capita growth rates decline as their relative abundance or frequency in a community increases, a pattern referred to as negative frequency dependence.

Negative frequency dependence is illustrated by the black lines in Fig. 1 for a hypothetical two-species system. To understand why stabilizing processes create a negative relationship between per capita growth rates and frequency, first consider the y -intercept, which represents the focal species’ per capita growth rate when it is rare and its competitor is at its single-species equilibrium. The more the resident competitor suppresses itself relative to the focal species, the more positive the focal species’ average growth rate when rare. Now consider how the focal species’ growth rate changes as its relative frequency in the community increases. The more the focal species suppresses itself compared with its competitor, the faster its per capita growth rate declines with frequency. Stronger stabilization therefore corresponds to more negative slopes. By contrast, when species suppress themselves and their competitors

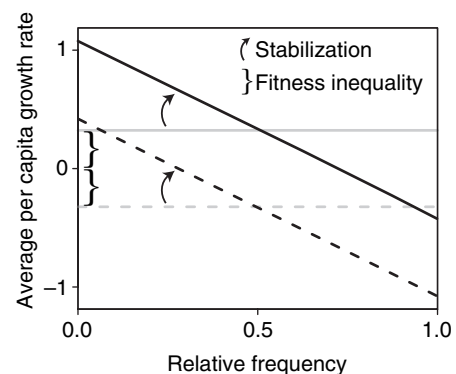


Figure 1 A negative slope in the relationship between per capita population growth rates and a species’ relative frequency in a community (black lines) show the degree of stabilization (niche differences) in a system. The difference between each species’ per capita population growth rate and zero in the absence of stabilization (grey lines) shows fitness inequality. Neutrality increases as fitness inequality decreases. The solid and dashed lines refer to two different hypothetical species.

equally, stabilization is absent, and the slopes are zero (the grey lines).

Our use of relative frequency on the x -axis in Fig. 1 should not imply that density-dependent processes are unimportant for coexistence. In fact, frequency dependence is almost always the product of density-dependence. The problem is that density dependence will emerge in any system with limited resources, but it will only translate into negative frequency dependence if species limit themselves more than they limit others. When community size is fixed, as in the neutral model, density and frequency are interchangeable, but as this case is rare, frequency is the appropriate metric for detecting stabilization. The link between frequency and diversity has a long history in population genetics, and negative frequency dependence is recognized as the signature of mechanisms maintaining genetic diversity (Ayala & Campbell 1974).

Although stabilizing mechanisms are what most ecologists associate with niche theory, a key message of Chesson (2000) is that these mechanisms alone do not ensure stable coexistence. Coexistence also depends on the magnitude of

the fitness difference or inequality between species. As shown in Box 1 and the central panel of Fig. 2, if fitness differences are large, strong stabilization is required for long-term coexistence. Conversely, if species are very similar in their fitness, even weak stabilizing effects can generate coexistence. It is the balance of fitness inequality and stabilizing, niche-based processes that determines coexistence (Box 1, Fig. 2).

What precisely are the fitness differences among species that are important from a coexistence perspective? The specific traits depend on the model used to describe coexistence. In the two-species lottery model of Snyder & Chesson (2003), fitness differences reflect differences in the product of the species' fecundity and their ability to capture space. In the annual plant model of Box 1, they are the fecundities, and in a resource competition model, they are differences in growth rates resulting from differences in R^* s (Chesson 2000). In all these models, however, fitness differences predict the outcome of competition in the absence of stabilizing processes (Chesson 2000). For example, if coexistence occurs because plants differ in the

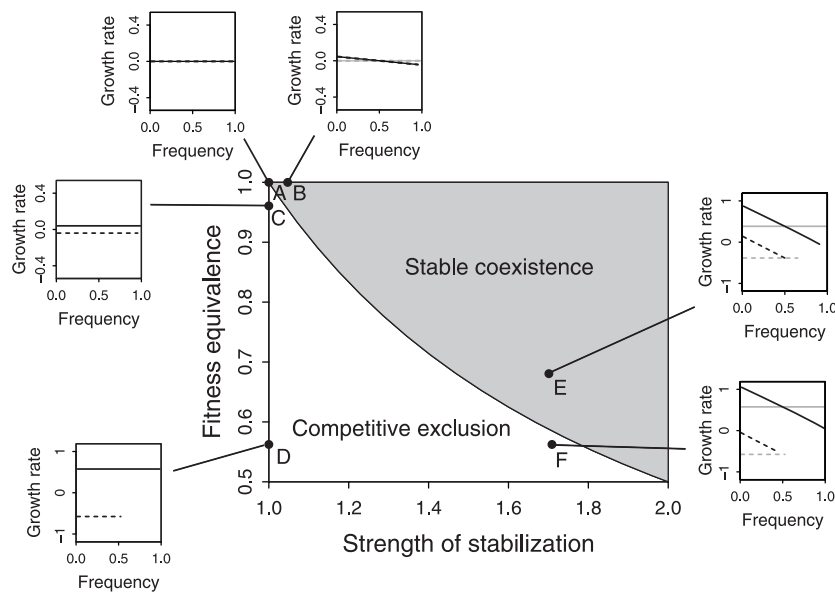


Figure 2 As equivalence in species' average fitness increases, the strength of stabilization necessary for long-term coexistence decreases. This relationship is illustrated in the special case of a two-species annual plant competition model (Box 1). We assume symmetric interspecific competition ($\alpha_{ij} = \alpha_{ji}$) and fixed intraspecific competition ($\alpha_{ii} = \alpha_{jj} = 1$) for illustrative purposes only. The y -axis shows the ratio λ_1/λ_2 , the fitness equivalence term for our specific model (Box 1). When $\lambda_2 > \lambda_1$, as in the figure, coexistence is possible when species 1 can increase when rare, which depends on the strength of stabilization, $\frac{\lambda_2}{1 + (\alpha_{12}/\alpha_{22})(\lambda_2 - 1)}$ (Box 1). This term is shown on the x -axis, and is a function of the degree to which species effect themselves vs. others, α_{12}/α_{22} . A value of one indicates the absence of stabilization. In the small panels, the black lines show the per capita population growth rates of the two competing species as a function of their relative frequency in the community. To generate these curves, we used eqns 1 and 2 to calculate the per capita population growth rate of a target species at densities ranging from near zero to its single-species carrying capacity. At each point along this gradient, we set the competitor species at its equilibrium density given the abundance of the target species, guaranteeing a fully saturated community. This explains why inferior competitors are never examined at 100% frequency. Finally, we converted densities to relative frequencies for the x -axis. The grey lines show the degree of fitness inequality. For (A–F), parameter values for $\lambda_1, \lambda_2, \alpha_{12} = \alpha_{21}$ are (A) 10, 10, 1; (B) 10, 10, 0.95; (C) 9.8, 10.2, 1; (D) 7.2, 12.8, 1; (E) 8.1, 11.9, 0.55; (F) 7.2, 12.8, 0.55. In every case, $\alpha_{11} = \alpha_{22} = 1$.

BOX 1: STABILIZATION AND FITNESS EQUIVALENCE IN A MODEL OF ANNUAL PLANT SPECIES

In any model of long-term coexistence, stabilizing processes and fitness equivalence both contribute to the coexistence of competing species. We illustrate this general principle with a two-species annual plant model (Watkinson 1980; Rees & Westoby 1997; Levine & Rees 2002), although the particular parameters that determine the degree of stabilization and fitness equivalence will vary from one model to another (Chesson 2000). The annual plant model describes the dynamics of two species:

$$N_{1,t+1} = \frac{\lambda_1 N_{1,t}}{1 + \alpha_{11} N_{1,t} + \alpha_{12} N_{2,t}}, \quad (1)$$

$$N_{2,t+1} = \frac{\lambda_2 N_{2,t}}{1 + \alpha_{22} N_{2,t} + \alpha_{21} N_{1,t}}. \quad (2)$$

In eqn 1, $N_{1,t+1}$ is the number or density of individuals of species 1 in year $t + 1$. It equals the density in year t multiplied by the intrinsic rate of increase (or fecundity), λ_1 divided by total competition. Competition is the sum of intraspecific and interspecific effects, determined by competition coefficients α_{11} and α_{12} respectively. α_{11} describes the per capita effect of an individual of species 1 on itself, while α_{12} describes the per capita effect of an individual of species 2 on species 1. The same interpretation of parameters follows for species 2.

The per capita growth rate of species 1 when it is rare and its competitor is at its single-species equilibrium

density ($(\lambda_2 - 1)/\alpha_{22}$) can be expressed as follows (swapping the 1 and 2 subscripts gives the expression for species 2):

$$\frac{N_{1,t+1}}{N_{1,t}} = \left(\frac{\lambda_1}{\lambda_2} \right) \left[\frac{\lambda_2}{1 + (\alpha_{12}/\alpha_{22})(\lambda_2 - 1)} \right], \quad (3)$$

where λ_1/λ_2 is the fitness inequality, describing the per capita population growth rate in the absence of stabilization (which occurs when $\alpha_{12} = \alpha_{22}$). If $\lambda_1 > \lambda_2$, species 1 wins in the absence of stabilizing mechanisms. If $\lambda_2 > \lambda_1$, species 2 wins. Although in this model, fitness inequality corresponds to variation in fecundity or the intrinsic rate of increase, we caution that in other models it will depend on other traits and processes.

For stable coexistence, both species must have a growth rate when rare that exceeds 1. However, unless the λ s are equivalent, the fitness equivalence term, λ_1/λ_2 , will always be < 1 for one of the two species. Thus, long-term coexistence is not possible without stabilization. In eqn 3, stabilization is expressed by the square bracketed term, a function of the degree to which intraspecific effects (α_{22}) exceed interspecific effects (α_{12}). When these terms are equal, the stabilization term equals 1 (it drops out); as the degree to which α_{22} exceeds α_{12} increases, stabilization grows increasingly positive. How large the stabilization term must be for coexistence depends on the fitness inequality of the two species. If the fitnesses are close to equal, only weak stabilization is required for coexistence. But as fitness differences increase, a larger stabilization term is required to generate coexistence (Fig. 2).

depth at which they obtain soil resources, fitness differences predict the winner when roots are distributed equally access the soil profile.

To estimate fitness differences, we need to know species' average per capita growth rates when intraspecific effects equal interspecific effects. When species have equal sensitivity to shared limiting factors, the difference in these growth rates is a measure of fitness inequality (the grey lines in Fig. 1). More generally, fitness inequality is the *scaled* difference in species' per capita growth rates in the absence of stabilization; the scaling terms reflect differences in how species' growth rates respond to shared limiting factors (Chesson & Huntly 1997; Chesson 2000; Snyder *et al.* 2005). In systems without any stabilization, the more the growth rates differ, the more rapidly species with negative growth rates will be excluded.

Because coexistence depends on both stabilizing processes and differences in average fitness, tradeoffs can promote

coexistence in two distinct ways (Chesson 2000). Stabilizing tradeoffs increase the strength of intra- relative to interspecific interactions. One well-known example is a tradeoff in species' ability to draw down two essential soil resources (Tilman 1982). However, tradeoffs can be equalizing when they reduce fitness differences between species without affecting the relative strength of intra- vs. interspecific effects. For instance, tradeoffs between fecundity and the ability to capture space (e.g. Turnbull *et al.* 1999) can be equalizing in a two-species lottery model (Snyder & Chesson 2003). Equalizing tradeoffs can promote diversity by reducing the strength of stabilizing processes necessary for stable coexistence.

THE NICHE FOR NEUTRALITY

As stabilizing processes and fitness inequality combine to determine coexistence, Hubbell's neutral model represents one of many possible scenarios for explaining the co-occur-

rence of species in natural communities. In the neutral model, species have identical average fitness and stabilizing mechanisms are completely absent. This scenario is labelled 'A' in Fig. 2. In the corresponding subpanel, lack of stabilization is shown by the horizontal growth curves, and fitness equivalence is indicated by the identical per capita population growth rates. Points 'B' and 'C' illustrate slight stabilization and slight fitness inequality respectively. Point 'D' shows species with large fitness differences and no stabilization. Points 'E' and 'F' combine differences in average fitness with strong stabilizing processes, but only in 'E' do the stabilizing processes overcome the fitness differences to generate stable coexistence. Figure 3 shows simulated dynamics typical for each of

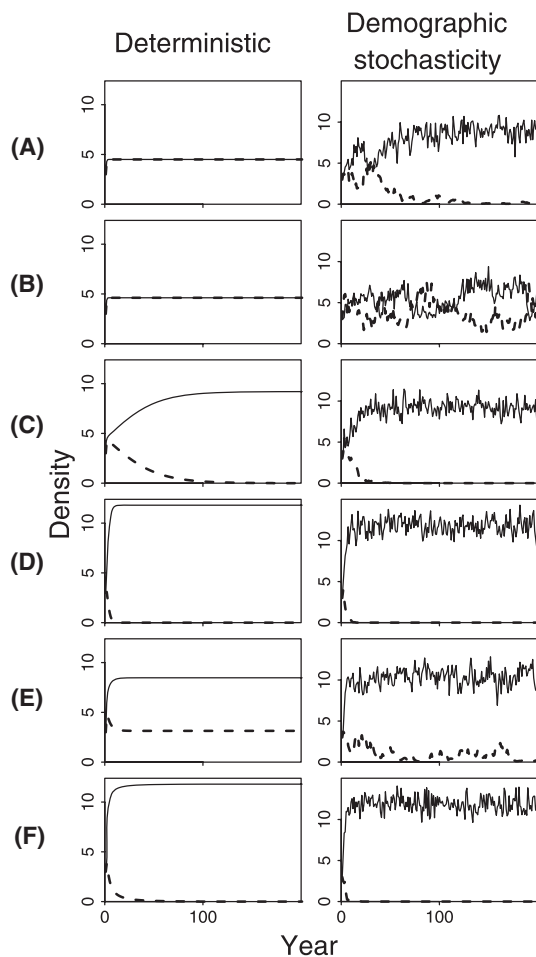


Figure 3 Simulated dynamics of two competing species depend on the strength of fitness equivalence and stabilization but also on demographic stochasticity. Scenarios (A–F) refer to labels in Fig. 2, and corresponding parameters are listed in its legend. The first column of figures is based on simulations of the deterministic model described in Box 1. The second column adds demographic stochasticity to these simulations by assuming that the λ values at each time step follow a Poisson distribution (we assume that the λ values are integers).

these scenarios. In the perfectly neutral case, species coexist (Fig. 3, row A), but this coexistence is inherently unstable because any deviation from fitness equivalence or demographic stochasticity leads to local extinction (as explained below). With differences in fecundity (Fig. 3, rows C and D), extinction occurs more rapidly unless strong stabilizing mechanisms are present (Fig. 3, row E).

After decades of research on coexistence, we still do not know where real communities fall in Fig. 2. We can, however, rule out a couple of scenarios. Given that species are not truly identical (Wootton 2005; Harpole & Tilman 2006), scenario 'A' is unlikely. We also know that 'D' cannot reflect diverse natural communities as it leads to very rapid competitive exclusion. The interesting question is whether natural communities lie near scenarios B and C or near E and F, or even combine strong stabilization and high fitness equivalence (the upper right corner in Fig. 2).

Although the examples in Figs 2 and 3 are for two-species models, coexistence in systems of many species is also driven by the combination of stabilizing processes and fitness equivalence: negative frequency-dependent growth describes stabilization, and per capita growth rate differences in the absence of stabilization describe fitness inequality. The same growth curves shown in Fig. 1 can be drawn for any number of species, with the x -axis showing the frequency of each focal species within the full community. Each slope reflects both the degree to which the focal species suppresses itself relative to the resident community, and the degree to which the resident community limits itself relative to the focal species. As in the two-species case, in the absence of stabilization, the growth rate of each focal species relative to zero provides a measure of fitness inequality. The multispecies case emphasizes that stabilization and fitness inequality are properties of individual species, not the whole community.

Placing the neutral model within classic coexistence theory emphasizes two important lessons:

- (1) Niche and neutral processes combine to generate coexistence. More precisely, communities can vary in both the strength of stabilization and the degree of fitness equivalence among species, as shown in Fig. 2. Because these two axes are orthogonal, it does not make sense to ask whether coexistence reflects either niche or neutral processes. Instead, we need to quantify both stabilization and fitness inequality, and then ask whether diversity is maintained by strong stabilizing processes overcoming large fitness inequality among species or weak stabilization operating on species with similar average fitness.
- (2) Relationships between per capita population growth rates and species' relative abundance in a community provide a basis for testing the relative contribution of

niches and neutrality to coexistence, as shown in Figs 1 and 2. Strong negative frequency dependence in per capita growth (steep negative slopes) indicates strong stabilizing mechanisms, or niches, whereas large differences in per capita growth rates when stabilization is absent indicate large fitness inequality (less neutrality).

DEMOGRAPHIC STOCHASTICITY AND DISPERSAL LIMITATION

The presence of demographic stochasticity and dispersal limitation is often regarded as a key indicator of neutrality (Hubbell 2001; Tuomisto *et al.* 2003; Gilbert & Lechowicz 2004; Tilman 2004; Hubbell 2005). After all, they are the only drivers of spatial and temporal variation in species' abundances in neutral communities. However, because demographic stochasticity and dispersal limitation have similar effects when included in niche-based models, they do not clearly distinguish the contribution of niches and neutrality to community structure.

Demographic stochasticity

Demographic stochasticity or chance variation in birth and death rates caused by the finite nature of populations, causes two phenomena in a neutral model. First, when all species have equivalent fitness and stabilizing mechanisms are absent (point A in Fig. 2), demographic stochasticity or 'ecological drift' is the only factor driving dynamics. Second, drift ultimately reduces local diversity (Fig. 3A). Still, the influence of demographic stochasticity does not reveal the relative role of niche and neutral processes, because it has the same effects in the presence of stabilizing mechanisms (Fig. 3E). If we ignore environmental stochasticity, as neutral models do, demographic stochasticity is the only factor causing variation in density through time in a stabilized community at equilibrium. And just as in the neutral model, species that coexist in our stabilized annual plant models are more extinction prone when demographic stochasticity is incorporated (Fig. 3E, Tilman 2004). Species with small population sizes due to deterministic factors will be especially sensitive to stochastic extinction.

How demographic stochasticity interacts with stabilizing mechanisms and fitness inequality to affect coexistence depends on community size, defined as the number of individuals in the community (the parameter J in Hubbell's model). When community size is large, species populations will tend to be large, and demographic stochasticity should only have a strong influence on dynamics if stabilization is very weak and fitness differences are small – systems close to true neutrality (point A in Fig. 2). In large communities further from neutrality, deterministic processes should overwhelm the effects of demographic stochasticity. But

as community size declines towards zero, drift can overwhelm even strong stabilizing effects and cause extinctions despite niche differences (Tilman 2004). Whether these drift-dominated communities are now 'neutral' may be a semantic point. What is clear is that demographic stochasticity does not quantitatively alter stabilizing processes or fitness equivalence, only their ability to buffer species from extinction in finite communities.

Dispersal limitation

Dispersal limitation has been used as a diagnostic for neutral community dynamics (e.g. Tuomisto *et al.* 2003; Gilbert & Lechowicz 2004). It occurs when the propagules of a species fail to arrive at all locations suitable for its growth, allowing competitively inferior species to win sites 'by default.' Dispersal limitation influences diversity in two ways in Hubbell's (2001) neutral model. First, increasing dispersal limitation between local communities within the larger metacommunity leads to greater isolation of the local communities. Isolation effectively reduces community size, leading to more extinctions through demographic stochasticity. Second, Hubbell (2001) argues that dispersal limitation slows the rate of competitive displacement within local communities when species are dissimilar in fitness. If superior species are unable to colonize all suitable habitats, the rate at which they displace inferior species will decrease.

Despite the potentially important role of dispersal limitation in neutral communities, in non-neutral communities dispersal limitation can contribute to stable coexistence. This result can occur when dispersal limitation interacts with spatial environmental heterogeneity, demographic stochasticity, or strong, asymmetric competition (Hurtt & Pacala 1995; Bolker & Pacala 1999; Levine & Rees 2002; Snyder & Chesson 2003). Dispersal limitation may also emerge in stabilized communities where coexistence occurs through mechanisms unrelated to spatial environmental variability (e.g. competition–colonization tradeoffs, the storage effect). Thus, evidence for strong dispersal limitation is a poor test of the relative importance of niche and neutral processes.

QUANTIFYING THE ROLE OF NICHES AND NEUTRALITY IN NATURAL COMMUNITIES

Here, we outline empirical approaches for determining the degree to which diversity is maintained by strong stabilizing processes overcoming large fitness differences among species, vs. weak stabilization acting on small fitness differences. Our goal was to focus on the cumulative effects of stabilizing processes and fitness inequality rather than individual coexistence mechanisms. This important departure from the mechanistic focus of classical coexist-

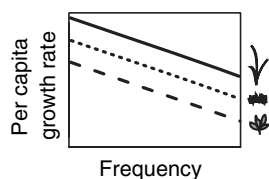
ence studies (e.g. Silvertown *et al.* 1999; McKane *et al.* 2002) will enable ecologists to answer the broader questions about fitness inequality and stabilization before identifying specific niche-based processes. In this section, we outline three sequential analyses for evaluating the role of stabilization and fitness equivalence in natural communities (Fig. 4). We present the analyses in the order of increasing power and data requirements, but we emphasize that even analysis 1 provides valuable information.

Analysis 1: quantify stabilization

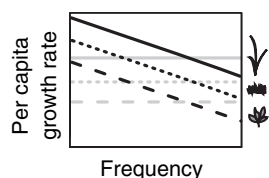
Because stabilizing mechanisms cause intraspecific effects to be more negative than interspecific effects, a simple test for the presence of stabilizing processes is to compare intra- and interspecific effects on vital rates such as germination, growth or survival for many co-occurring species. Many

Analyses

1. Quantify stabilization



2. Compare stabilization to fitness inequality



3. Remove stabilization to test its importance for coexistence

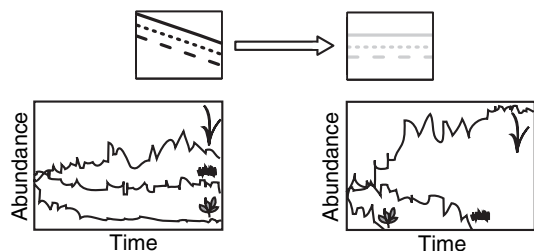


Figure 4 Three analyses for testing the relative role of stabilizing mechanisms and fitness equivalence in structuring natural communities. Experimental manipulations or monitoring combined with simulation models could be used for each of the three analyses. Each analysis allows increasingly stronger conclusions about the relative importance of stabilizing mechanisms (niches) and fitness equivalence (neutrality).

tropical and temperate trees do in fact limit their own establishment (Harms *et al.* 2000; HilleRisLambers *et al.* 2002) and survival (Wills *et al.* 2006) more than they are limited by other species. These results provide evidence that species interactions are not neutral, and suggest stabilization. However, because stabilizing processes operating on one-life stage could be offset by destabilizing effects at another, we do not know the degree to which per capita population growth rates are buffered. In addition, this approach tends to focus on how species *respond* to conspecific vs. heterospecific densities. A subtle, but critical point by Chesson (2000), is that stabilization results from differences in species *effects* on themselves vs. *effects* on others, not their responses (e.g. see Box 1).

To describe stabilization more rigorously, one first needs to integrate intra- and interspecific effects across all life stages to get information on frequency-dependent per capita growth rates, as in Figs 1 and 4. A challenge in attempting this with observational data is that the range of relative abundances occurring naturally is likely to be small. Simply plotting observed growth rates against observed frequency will rarely give a satisfactory description of the frequency–growth rate relationship. However, one could use observational data and statistical methods to fit the parameters of a model that describes how each species' growth rate depends on the composition of the surrounding community (e.g. Rees *et al.* 1996; Freckleton & Watkinson 2001; Adler *et al.* 2006). The model parameters could then be used to project per capita growth rates across a wide range of relative frequencies. We outline this approach in more detail under analysis 2.

An alternative is to assemble experimental communities and directly measure per capita population growth rates. This is especially feasible for communities of annual plants (Turnbull *et al.* 2005). To measure growth rates across a wide range of relative frequencies, plots could be seeded with different frequencies of a focal species and its background community. When implementing this approach, there are at least two important considerations. First, manipulations need to be maintained long enough for the composition of the background community to adjust in response to the density of the focal species. Second, manipulations need to be performed over scales that are broad enough to capture any environmental heterogeneity (spatial and temporal) important in generating the stabilizing processes operating in the community.

Quantitative measures of stabilization can address a variety of interesting questions. The most basic question is whether stabilizing processes contribute to coexistence. We could also ask how experimental treatments such as nutrient addition or herbivore removal change the overall strength of stabilization, or whether common and rare species tend to differ within a community. Interesting cross-system comparisons will also be possible once the relationship between

frequency and per capita growth rates is described for a variety of communities. For example, we could test Chesson's (2000) prediction that as the number of species in a system increases the strength of stabilization will decrease (less negative frequency dependence). However, information on stabilization alone cannot address questions about the relative importance of niche vs. neutral processes, as this also requires a measure of fitness inequality.

Analysis 2: quantify fitness inequality and compare with stabilization

Quantifying fitness inequality is more difficult than quantifying stabilization, and is a rapidly developing research area. The approach we advocate is to use observational or experimental data to estimate the parameters of a relatively simple model which can be decomposed into fitness inequality and stabilization terms (as in Box 1 or Chesson 2000). The first step is obtaining data on population growth rates as a function of the density of other species in the surrounding community. The next step is fitting a phenomenological model that includes terms for intraspecific interactions (e.g. α_{11} and α_{22} in Box 1), interspecific interactions (α_{12} and α_{21} in Box 1), and per capita growth rates in the absence of density effects (the λ s in Box 1). Even though the model in Box 1 was originally intended for annual plant communities, it could also be used to model annual changes in biomass or per cent cover in perennial communities (with a slightly different biological interpretation of the parameters).

Estimating these model parameters will typically require statistical techniques such as maximum likelihood or Bayesian hierarchical models (Rees *et al.* 1996; Freckleton & Watkinson 2001; Adler *et al.* 2006). Estimation can be simplified by modelling one target species in competition with the aggregate community, essentially turning a many-species community into a series of two-species systems, and repeating the process for each species of interest in the community.

Once parameters are estimated, fitness inequality for a species can be calculated based on per capita growth rates after setting intraspecific effects equal to interspecific effects. For the model described in Box 1, this calculation gives the ratio of the λ s as the fitness inequality measure. For examples based on other models, and for the appropriate scaling of growth rates when species differ in their sensitivities to common limiting factors, see Chesson & Huntly (1997), Chesson (2000) and Snyder *et al.* (2005). The strength of the stabilization term can also be calculated from the model parameters. This overall approach differs from that of Hallett & Pimm (1979) (see critique by Bender *et al.* 1984) because we recommend fitting a full population model for each species rather than simply estimating competition coefficients from deviations around the multispecies equilibrium.

Quantitative estimates of fitness inequality and stabilization in a natural community directly address the relative importance of niche and neutral processes (as in Fig. 1). However, conclusions based on model parameters reflect a deterministic perspective, and ignore the influence of demographic stochasticity and some effects of dispersal limitation on coexistence. Even in cases where the fitted parameters indicate stable coexistence, population sizes in natural systems may be small enough that stochasticity overwhelms stabilization, causing local extinctions (e.g. Fig. 3E). On the other hand, when the parameters predict competitive exclusion, dispersal limitation may allow species to co-occur for long periods. To determine the net effect of fitness inequality and stabilization on coexistence in the presence of stochastic influences, we need analyses or experiments that incorporate all these factors.

Analysis 3: remove stabilization to test its importance for coexistence

We can evaluate the consequences of stabilizing mechanisms and fitness equivalence for coexistence in finite populations by manipulating the strength of stabilization and quantifying the number and rate of local extinctions. The more important stabilizing mechanisms are for coexistence, the more rapidly their removal will increase extinction rates. In practice, removing stabilization means forcing the frequency–population growth relationship to be horizontal for each species at a level set by their fitness inequality (Fig. 4). To remove stabilizing effects from an empirically parameterized, stochastic version of the annual plant model, we would manipulate the α s so that intra- and interspecific effects are equal for each species. We could then compare the number and rate of extinctions in simulations based on the empirical α values and the altered α values. Of course, an important prerequisite for this manipulation is reliable estimates of the strength of stabilizing processes and fitness inequality.

One can also remove stabilizing effects with an experimental approach, at least for short-lived species. If stabilizing mechanisms affect population dynamics in mixtures of annual plants, then per capita seed production will be relatively high when species are rare and relatively low when they are common. To force the relationship between per capita seed production and frequency for each species to become flat, in effect removing stabilization, one could manipulate seed production at the plot level. When a species becomes rare in a plot, seeds would be removed to reduce its growth rate, whereas seeds would be added to plots where a species is relatively common. The precise amount of seeds removed or added would be set by each species' frequency-independent per capita growth rate in the absence of stabilizing mechanisms – their fitness inequalities

determined from analysis 2. If stabilizing processes are very important, diversity in these manipulated plots would decrease faster than in unmanipulated plots. If species have similar average fitness, diversity would remain relatively high even in the absence of stabilizing processes. It is possible that local extinctions may not occur for many years, even in the 'stabilization removal' treatment. In this case, demographic data collected in the experimental treatments could be used to parameterize long-running simulations.

Summary of empirical tests

The analyses we have outlined require considerable data on species' performance and interactions across wide ranges of biotic and abiotic variabilities, and also sophisticated quantitative techniques. It should be no surprise that answering the niche vs. neutrality question will be difficult, but we are confident that community ecologists can rise to the challenge. A number of long-term data sets on community dynamics already exist (e.g. Ernest & Brown 2001; Wootton 2005; Adler *et al.* 2006; Wills *et al.* 2006), and a revolution in statistical computing has made it possible to estimate complex nonlinear processes with these data (Clark 2005). Finally, the same manipulations used in biodiversity–ecosystem function experiments (e.g. Tilman *et al.* 1996) could quantify frequency-dependent growth, at least for communities of short-lived organisms.

CONCLUSIONS

Because niche and neutral theories focus on complementary processes that control community dynamics, each theory strengthens our understanding of the other. Locating neutral theory within classic coexistence theory emphasizes that the principles underlying neutrality are well established. In return, neutral theory can help refine the niche paradigm by focusing our attention on fitness equivalence and emphasizing that in many natural communities niche differences may be more subtle than traditionally expected yet still generate stable coexistence. Further empirical work will show how stabilizing processes and fitness inequality vary among communities and respond to anthropogenic changes.

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REFERENCES

- Adler, P.B., HilleRisLambers, J., Kyriakidis, P., Guan, Q. & Levine, J.M. (2006). Climate variability has a stabilizing effect on coexistence of prairie grasses. *Proc. Natl Acad. Sci. USA*, 103, 12793–12798.
- Ayala, F.J. & Campbell, C.A. (1974). Frequency dependent selection. *Annu. Rev. Ecol. Syst.*, 5, 115–138.
- Bell, G. (2000). The distribution of abundance in neutral communities. *Am. Nat.*, 155, 606–617.
- Bell, G. (2001). Neutral macroecology. *Science*, 293, 2413–2418.
- Bell, G. (2005). The co-distribution of species in relation to the neutral theory of community ecology. *Ecology*, 86, 1757–1770.
- Bender, E.A., Case, T.J. & Gilpin, M.E. (1984). Perturbation experiments in community ecology: theory and practice. *Ecology*, 65, 1–13.
- Bolker, B.M. & Pacala, S.W. (1999). Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.*, 153, 575–602.
- Caceres, C.E. (1997). Temporal variation, dormancy, and coexistence: a field test of the storage effect. *Proc. Natl Acad. Sci. USA*, 94, 9171–9175.
- Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.
- Chave, J., Muller-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.
- Chesson, P. & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.*, 150, 519–553.
- Clark, J.S. (2005). Why environmental scientists are becoming Bayesians. *Ecol. Lett.*, 8, 2–14.
- Ernest, S.K.M. & Brown, J.H. (2001). Delayed compensation for missing keystone species by colonization. *Science*, 292, 101–104.
- Freckleton, R.P. & Watkinson, A.R. (2001). Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life history traits. *Ecol. Lett.*, 4, 348–357.
- Gilbert, B. & Lechowicz, M.J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. *Proc. Natl Acad. Sci.*, 101, 7651–7656.
- Grant, P.R. (1986). *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton, NJ.
- Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006). Reconciling niche and neutrality: the continuum hypothesis. *Ecol. Lett.*, 9, 399–409.
- Grubb, P.J. (1977). The maintenance of species richness in plant communities. The importance of the regeneration niche. *Biol. Rev.*, 52, 107–145.
- Hallett, J.G. & Pimm, S.L. (1979). Direct estimation of competition. *Am. Nat.*, 113, 593–600.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404, 493–495.
- Harpole, W.S. & Tilman, D. (2006). Non-neutral patterns of species abundance in grassland communities. *Ecol. Lett.*, 9, 15–23.
- HilleRisLambers, J., Clark, J.S. & Beckage, B. (2002). Density-dependent mortality and the latitudinal gradient in species diversity. *Nature*, 417, 732–735.

- 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.
- Hurttt, 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.
- Leibold, M.A. & McPeck, M.A. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, 87, 1399–1410.
- Levine, J.M. & Rees, M. (2002). Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *Am. Nat.*, 160, 452–467.
- McGill, B.J. (2003a). A test of the unified neutral theory of biodiversity. *Nature*, 422, 881–885.
- McGill, B.J. (2003b). Strong and weak tests of macroecological theory. *Oikos*, 102, 679–685.
- McKane, R.B., Johnson, L.C., Shaver, G.S., Nadelhoffer, K.J., Rastetter, E.B., Fry, B. *et al.* (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415, 68–71.
- Purves, D.W. & Pacala, S.W. (2005). Ecological drift in niche-structured communities: neutral pattern does not imply neutral process. In: *Biotic Interactions in the Tropics* (eds Burslem, D., Pinard, M. & Hartley, S.). Cambridge University Press, Cambridge, UK, pp. 103–138.
- Rees, M. & Westoby, M. (1997). Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos*, 78, 116–126.
- Rees, M., Grubb, P.J. & Kelley, D. (1996). Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *Am. Nat.*, 147, 1–32.
- Rees, M., Condit, R., Crawley, M., Pacala, S. & Tilman, D. (2001). Long-term studies of vegetation dynamics. *Science*, 293, 650–655.
- Silvertown, J. (2004). Plant coexistence and the niche. *Trends Ecol. Evol.*, 19, 605–611.
- Silvertown, J., Dodd, M.E., Gowing, D.J.G. & Mountford, J.O. (1999). Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature*, 400, 61–63.
- Silvertown, J., McConway, K., Gowing, D., Dodd, M., Fay, M.F., Joseph, J.A. *et al.* (2006). Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proc. R. Soc. Lond. B, Biol. Sci.*, 273, 39–44.
- Snyder, R.E. & Chesson, P. (2003). Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecol. Lett.*, 6, 301–309.
- Snyder, R.E., Borer, E.T. & Chesson, P. (2005). Examining the relative importance of spatial and nonspatial coexistence mechanisms. *Am. Nat.*, 166, E75–E94.
- 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.
- Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299, 241–244.
- Turnbull, L.A., Rees, M. & Crawley, M.J. (1999). Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.*, 87, 899–912.
- Turnbull, L.A., Manley, L. & Rees, M. (2005). Niches, rather than neutrality, structure a grassland pioneer guild. *Proc. R. Soc. Lond. B, Biol. Sci.*, 272, 1357–1364.
- Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424, 1035–1037.
- Volkov, I., Banavar, J.R., He, F.L., Hubbell, S.P. & Maritan, A. (2005). Density dependence explains tree species abundance and diversity in tropical forests. *Nature*, 438, 658–661.
- Watkinson, A.R. (1980). Density-dependence in single-species populations of plants. *J. Theor. Biol.*, 83, 345–357.
- Wills, C., Harms, K.E., Condit, R., King, D., Thompson, J., He, F.L. *et al.* (2006). Nonrandom processes maintain diversity in tropical forests. *Science*, 311, 527–531.
- Wootton, J.T. (2005). Field parameterization and experimental test of the neutral theory of biodiversity. *Nature*, 433, 309–312.
- Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, 130, 1–14.

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