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2 **A niche for neutrality**3 Peter B. Adler¹, Janneke HilleRisLambers², Jonathan M. Levine³

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1 **Abstract**

2 Ecologists now recognize that controversy over the relative importance of niches and neutrality
3 cannot be resolved with current analyses of species abundance patterns. Here we use classical
4 coexistence theory to reframe the debate in terms of stabilizing mechanisms (niches) and fitness
5 equivalence (neutrality). The neutral model is a special case where stabilizing mechanisms are
6 absent and species have equivalent fitness. Instead of asking whether niches or neutral processes
7 structure communities, we advocate determining the degree to which observed diversity reflects
8 strong stabilizing mechanisms overcoming large fitness differences or weak stabilization
9 operating on species of similar fitness. To answer this question, we propose combining data on
10 per capita growth rates with models to 1) quantify the strength of stabilizing processes, 2)
11 quantify fitness inequality and compare it to stabilization, and 3) manipulate frequency-
12 dependence in growth to test the consequences of stabilization and fitness equivalence for
13 coexistence.

14

1 **Introduction**

2
3 Much of ecology is built on the assumption that species differ in their niches. Classic
4 studies have shown that species may differ in their use of multiple limiting resources (Tilman
5 1982, Grant 1986), their ability to colonize disturbed sites (Grubb 1977), and their response to
6 temporal fluctuations in the environment (Caceres 1997). In theory, niche differences cause
7 species to limit their own populations more than they limit others, promoting coexistence
8 (Chesson 2000). But despite the overwhelming evidence for niche differences (reviewed in Rees
9 et al. 2001, Wright 2002), few studies have successfully quantified their importance for
10 maintaining the diversity we observe in natural communities (Silvertown 2004). This gap in the
11 empirical evidence for niche-based coexistence has been highlighted by the recent emergence of
12 a competing explanation for the maintenance of diversity.

13 Neutral theory (Bell 2000, Hubbell 2001) directly challenges the niche paradigm by
14 proposing that species similarities, not differences, explain the high diversity of many natural
15 communities. Neutral models are built on the assumption that all species are identical in their
16 fitness and in their effects on one another. The niche mechanisms that ecologists have studied
17 intensively for decades play no role in neutral models, and the only driver of population
18 dynamics is random variation in births, deaths, and dispersal. In the absence of speciation, these
19 stochastic events would eventually drive all but one species extinct, but high diversity can occur
20 in neutral communities if extinction rates are slow enough to be balanced by speciation.

21 Despite their extreme assumptions about species equivalence, neutral models have
22 successfully reproduced fundamental ecological patterns such as species-area relationships and
23 species abundance distributions (Bell 2000, Bell 2001, Hubbell 2001). In fact, the species
24 abundance distribution (SAD) predicted by Hubbell's neutral model describes some empirical

1 SADs better than distributions associated with niche theory (Hubbell 2001, McGill 2003a,
2 Volkov et al. 2003). Proponents of the neutral model have interpreted these results as evidence
3 that demographic stochasticity and dispersal limitation can be more important than functional
4 differences among species for generating community patterns (Hubbell 2005).

5 More recent work, however, has emphasized the difficulty of identifying underlying
6 processes from patterns like the SAD. Although the fitting of SADs remains controversial, all
7 parties now agree that niche and neutral models can generate very similar patterns (Chave et al.
8 2002, Chave 2004, Bell 2005, Purves & Pacala 2005, Volkov et al. 2005). This renders “curve
9 fitting” a weak approach for establishing the relative importance of niche and neutral processes
10 in structuring communities, a fundamental goal of neutral theory (Hubbell 2001, McGill 2003b).
11 Our objective in this paper is to offer an alternative framework and empirical approach for
12 reaching this important goal. We focus primarily on plant communities, reflecting our own
13 experience, but our recommendations should apply to any community of “trophically similar,
14 sympatric species that actually or potentially compete...for the same or similar resources”
15 (Hubbell 2001).

16 In this paper we highlight key axes on which niche and neutral theory make unique,
17 testable predictions by focusing on coexistence—the heart of the debate. We first locate
18 “neutrality” within the framework of Chesson (2000), which treats coexistence as the outcome of
19 stabilizing mechanisms and fitness inequality. This synthesis of neutral theory with the classical
20 coexistence literature highlights a critical but unexplored question, “To what extent does the
21 diversity we observe in natural communities result from strong stabilizing mechanisms (niches)
22 overcoming large fitness differences versus weak stabilization operating on species of similar
23 fitness (neutrality)?” Because current analyses of static community patterns cannot answer this

1 question, we outline a series of empirical tests based on population growth rates to quantify
2 stabilizing processes and fitness inequality in nature.

3

4 **The Chesson lesson: classical coexistence theory and neutrality**

5 Niche and neutral theory are often treated as mutually exclusive explanations for
6 empirical patterns. This false dichotomy obscures the fact that niche and neutral processes
7 simultaneously influence the dynamics of competing species (Hubbell 2001, Bell 2001, Tilman
8 2004, Gravel et al. 2006, Leibold & McPeck 2006, Silvertown et al. 2006), and also implies that
9 classical niche theory has ignored the role of species' similarities in promoting coexistence. In
10 fact, classical theory treats coexistence as the result of both similarities and differences between
11 species. Chesson (2000) formalized this view, showing that the magnitude of niche-based
12 differences necessary to stabilize long-term coexistence depends on how similar species are in
13 average fitness. Neutral models are simply the special case where species have equivalent
14 fitness and there are no stabilizing, niche-based processes.

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

1 capita growth rates decline as their relative abundance or frequency in a community increases, a
2 pattern referred to as negative frequency dependence.

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

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

1 Although stabilizing mechanisms are what most ecologists associate with niche theory, a
2 key message of Chesson (2000) is that these mechanisms alone do not ensure stable coexistence.
3 Coexistence also depends on the magnitude of the fitness difference or inequality between
4 species. As shown in Box 1 and the central panel of Fig. 2, if fitness differences are large, strong
5 stabilization is required for long-term coexistence. Conversely, if species are very similar in
6 their fitness, even weak stabilizing effects can generate coexistence. It is the balance of fitness
7 inequality among species and stabilizing, niche-based processes that determines coexistence
8 (Box 1, Fig. 2).

9 What precisely are the fitness differences among species that are important from a
10 coexistence perspective? The specific traits depend on the model used to describe coexistence.
11 In the two species lottery model of Snyder and Chesson (2003), fitness differences reflect
12 differences in the product of the species' fecundity and their ability to capture space. In the
13 annual plant model of Box 1, they are the fecundities, and in a resource competition model, they
14 are differences in growth rates resulting from differences in R^* 's (Chesson 2000). In all of these
15 models, however, fitness differences predict the outcome of competition in the absence of
16 stabilizing processes (Chesson 2000). To estimate fitness differences, we need to know species'
17 average per capita growth rates in the absence of stabilizing processes. When species have equal
18 sensitivity to shared limiting factors, the difference in these growth rates is a measure of fitness
19 inequality (the gray lines in Fig. 1). More generally, fitness inequality is the *scaled* difference in
20 species' per capita growth rates in the absence of stabilization; the scaling terms reflect
21 differences in species' sensitivities to shared limiting factors (Chesson and Huntly 1997, Chesson
22 2000, Snyder et al. 2005). In systems without any stabilization, the more the growth rates differ,
23 the more rapidly species with negative growth rates will be excluded.

1 Because coexistence depends on both stabilizing processes and differences in average
2 fitness, trade-offs can promote coexistence in two distinct ways (Chesson 2000). Stabilizing
3 trade-offs increase the strength of intra- relative to interspecific interactions. One well-known
4 example is a trade-off in species' ability to draw down two essential soil resources (Tilman
5 1982). However, trade-offs can be equalizing when they reduce fitness differences between
6 species without affecting the relative strength of intra- versus interspecific effects. For instance,
7 trade-offs between fecundity and the ability to capture space (e.g. Turnbull et al. 1999) can be
8 equalizing in a two species lottery model (Snyder & Chesson 2003). Equalizing trade-offs can
9 facilitate diversity-maintenance by reducing the strength of stabilizing processes necessary for
10 stable coexistence.

11 *The niche for neutrality*

12 Since stabilizing processes and fitness inequality combine to determine coexistence,
13 Hubbell's neutral model represents one of many possible scenarios for explaining the co-
14 occurrence of species in natural communities. In the neutral model, species have identical
15 average fitness and stabilizing mechanisms are completely absent. This scenario is labeled "A"
16 in Fig. 2. In the corresponding subpanel, lack of stabilization is shown by the horizontal growth
17 curves, and fitness equivalence is indicated by the identical per capita population growth rates.
18 Points "B" and "C" illustrate slight stabilization and slight fitness inequality, respectively. Point
19 "D" shows species with large fitness differences and no stabilization. Points "E" and "F"
20 combine differences in average fitness with strong stabilizing processes, but only in "E" do the
21 stabilizing processes overcome the fitness differences to generate stable coexistence. Fig. 3
22 shows simulated dynamics typical for each of these scenarios. In the perfectly neutral case,
23 species coexist (Fig. 3 row A), but this coexistence is inherently unstable because any deviation

1 from fitness equivalence or demographic stochasticity leads to local extinction (as explained
2 below). With differences in fecundity (Fig. 3 row C and D), extinction occurs more rapidly
3 unless strong stabilizing mechanisms are present (Fig. 3 row E).

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

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

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

1 1. Niche and neutral processes combine to generate coexistence. More precisely, communities
2 can vary in both the strength of stabilization and the degree of fitness equivalence among
3 species, as shown by Fig. 2. Because these two axes are orthogonal, it does not make sense to
4 ask whether coexistence reflects either niche or neutral processes. Instead, we need to quantify
5 both stabilization and fitness inequality, and then ask whether diversity is maintained by strong
6 stabilizing processes overcoming large fitness inequality among species or weak stabilization
7 operating on species with similar average fitness.

8 2. Relationships between per capita population growth rates and species' relative abundance in a
9 community provide a basis for testing the relative contribution of niches and neutrality to
10 coexistence, as shown in Fig. 1 and Fig. 2. Strong negative frequency-dependence in per capita
11 growth (steep negative slopes) indicates strong stabilizing mechanisms, or niches, whereas large
12 differences in per capita growth rates when stabilization is absent indicate large fitness inequality
13 (less neutrality).

14

15 **Demographic stochasticity and dispersal limitation**

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

22

23 *Demographic stochasticity*

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

14 How demographic stochasticity interacts with stabilizing mechanisms and fitness
15 inequality to affect coexistence depends on the number of individuals in the community, the
16 parameter J in Hubbell's model. When J is large, species populations will tend to be large, and
17 demographic stochasticity should only have a strong influence on dynamics if stabilization is
18 very weak and fitness differences are small—systems close to true neutrality (point A in Fig. 2).
19 In communities with large J further from neutrality, deterministic processes should overwhelm
20 the effects of demographic stochasticity. But as J declines towards zero, drift can overwhelm
21 even strong stabilizing effects and cause extinctions despite niche differences (Tilman 2004).
22 Whether these drift-dominated communities are now “neutral” may be a semantic point. What is

1 clear is that demographic stochasticity does not quantitatively alter stabilizing processes or
2 fitness equivalence, only their ability to buffer species from extinction in finite communities.

3 *Dispersal limitation*

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

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

23

1 **Quantifying the role of niches and neutrality in natural communities**

2 Here we outline empirical approaches for determining the degree to which diversity is
3 maintained by strong stabilizing processes overcoming large fitness differences among species,
4 versus weak stabilization acting on small fitness differences. Our goal is to focus on the
5 cumulative effects of stabilizing processes and fitness inequality rather than individual
6 coexistence mechanisms. This important departure from the mechanistic focus of classical
7 coexistence studies (e.g. Silvertown et al. 1999, McKane et al. 2002) will enable ecologists to
8 answer the broader questions about fitness inequality and stabilization before identifying specific
9 niche-based processes. In this section we outline three sequential analyses for evaluating the role
10 of stabilization and fitness equivalence in natural communities (Fig. 4). We present the analyses
11 in order of increasing power and data requirements, but we emphasize that even Analysis 1
12 provides valuable information.

13 *Analysis 1: Quantify stabilization*

14 Because stabilizing mechanisms cause intraspecific effects to be more negative than
15 interspecific effects, a simple test for the presence of stabilizing processes is to compare intra-
16 and interspecific effects on vital rates such as germination, growth, or survival for many co-
17 occurring species. Many tropical and temperate trees do in fact limit their own establishment
18 (Harms et al. 2000, Hille Ris Lambers et al. 2002) and survival (Wills et al. 2006) more than they
19 are limited by other species. These results provide evidence that species interactions are not
20 neutral, and suggest stabilization. However, because stabilizing processes operating on one life
21 stage could be offset by destabilizing effects at another, we do not know the degree to which per
22 capita population growth rates are buffered. In addition, this approach tends to focus on how
23 species *respond* to conspecific versus heterospecific densities. A subtle, but critical point made

1 in Chesson (2000), is that stabilization results from differences in species *effects* on themselves
2 versus *effects* on others, not their responses (see Box 1 for example).

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

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

1 Quantitative measures of stabilization can address a variety of interesting questions. The
2 most basic question is whether stabilizing processes contribute to coexistence. We could also
3 ask how experimental treatments such as nutrient addition or herbivore removal change the
4 overall strength of stabilization, or whether common and rare species tend to differ within a
5 community. Interesting cross-system comparisons will also be possible once the relationship
6 between frequency and per capita growth rates is described for a variety of communities. For
7 example, we could test Chesson's (2000) prediction that as the number of species in a system
8 increases the strength of stabilization will decrease (less negative frequency-dependence).
9 However, information on stabilization alone cannot address questions about the relative
10 importance of niche vs. neutral processes, since this also requires a measure of fitness inequality.

11 *Analysis 2: Quantify fitness inequality and compare to stabilization*

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

1 Estimating these model parameters will typically require statistical techniques such as
2 maximum likelihood or Bayesian hierarchical models (Rees et al. 1996, Freckleton & Watkinson
3 2001, Adler et al. 2006). Estimation can be simplified by modeling one target species in
4 competition with the aggregate community, essentially turning a many-species community into a
5 series of two species systems, and repeating the process for each species of interest in the
6 community.

7 Once parameters are estimated, fitness inequality for a species can be calculated based on
8 per capita growth rates after setting intraspecific effects equal to interspecific effects. For the
9 model described in Box 1, this calculation gives the ratio of the λ 's as the fitness inequality
10 measure. For examples based on other models, and for the appropriate scaling of growth rates
11 when species differ in their sensitivities to common limiting factors, see Chesson and Huntly
12 (1997), Chesson (2000), and Snyder et al. (2005). The strength of the stabilization term can also
13 be calculated from the model parameters. This overall approach differs from that of Hallett and
14 Pimm (1979) (see critique by Bender et al. 1984) because we recommend fitting a full population
15 model for each species rather than simply estimating competition coefficients from deviations
16 around the multispecies equilibrium.

17 Quantitative estimates of fitness inequality and stabilization in a natural community
18 directly address the relative importance of niche and neutral processes (as in Fig. 1). However,
19 conclusions based on model parameters reflect a deterministic perspective, and ignore the
20 influence of demographic stochasticity and some effects of dispersal limitation on coexistence.
21 Even in cases where the fitted parameters indicate stable coexistence, population sizes in natural
22 systems may be small enough that stochasticity overwhelms stabilization, causing local
23 extinctions (e.g. Fig. 3E). On the other hand, when the parameters predict competitive exclusion,

1 dispersal limitation may allow species to co-occur for long periods. To determine the net effect
2 of fitness inequality and stabilization on coexistence in the presence of stochastic influences, we
3 need analyses or experiments that incorporate all of these factors.

4 *Analysis 3: Remove stabilization to test its importance for coexistence*

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

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

1 frequency independent per capita growth rate in the absence of stabilizing mechanisms – their
2 fitness inequalities determined from Analysis 2. If stabilizing processes are very important,
3 diversity in these manipulated plots would decrease faster than in unmanipulated plots. If species
4 have similar average fitness, diversity would remain relatively high even in the absence of
5 stabilizing processes. It is possible that local extinctions may not occur for many years, even in
6 the “stabilization removal” treatment. In this case, demographic data collected in the
7 experimental treatments could be used to parameterize long-running simulations.

8 *Summary of empirical tests*

9 The analyses we have outlined require considerable data on species’ performance and
10 interactions across wide ranges of biotic and abiotic variability, and also sophisticated
11 quantitative techniques. It should be no surprise that answering the niche vs. neutrality question
12 will be difficult, but we are confident that community ecologists can rise to the challenge. A
13 number of long-term datasets on community dynamics already exist (e.g. Ernest & Brown 2001,
14 Wootton 2005, Wills et al. 2006, Adler et al. 2006), and a revolution in statistical computing has
15 made it possible to estimate complex nonlinear processes with these data (Clark 2005). Finally,
16 the same manipulations used in biodiversity-ecosystem function experiments (e.g. Tilman et al.
17 1996) could quantify frequency-dependent growth, at least for communities of short-lived
18 organisms.

19

20 **Conclusions**

21 Because niche and neutral theory focus on complementary processes that control
22 community dynamics, each theory strengthens our understanding of the other. Locating neutral
23 theory within classic coexistence theory emphasizes that the principles underlying neutrality are

1 well-established. In return, neutral theory can help refine the niche paradigm by focusing our
2 attention on fitness equivalence and emphasizing that in many natural communities niche
3 differences may be more subtle than traditionally expected yet still generate stable coexistence.
4 Further empirical work will show how stabilizing processes and fitness inequality vary among
5 communities and respond to anthropogenic changes.

6

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1 **Box 1: Stabilization and fitness equivalence in a model of annual plant species**

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

$$8 \quad N_{1,t+1} = \frac{\lambda_1 N_{1,t}}{1 + \alpha_{11} N_{1,t} + \alpha_{12} N_{2,t}} \quad (1)$$

$$9 \quad N_{2,t+1} = \frac{\lambda_2 N_{2,t}}{1 + \alpha_{21} N_{1,t} + \alpha_{22} N_{2,t}} \quad (2)$$

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

16 The per capita growth rate of species one when it is rare and its competitor is at its single
 17 species equilibrium density $\left(\frac{\lambda_2 - 1}{\alpha_{22}} \right)$ can be expressed as follows (swapping the 1 and 2
 18 subscripts gives the expression for species 2):

$$19 \quad \frac{N_{1,t+1}}{N_{1,t}} = \left(\frac{\lambda_1}{\lambda_2} \right) \left[\frac{\lambda_2}{1 + \left(\frac{\alpha_{12}}{\alpha_{22}} \right) (\lambda_2 - 1)} \right] \quad (3)$$

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

6 For stable coexistence, both species must have a growth rate when rare that exceeds one.

7 However, unless the λ 's are equivalent, the fitness equivalence term, $\frac{\lambda_1}{\lambda_2}$, will always be less
8 than one for one of the two species. Thus, long-term coexistence is not possible without
9 stabilization. In equation 3, stabilization is expressed by the square bracketed term, a function of
10 the degree to which intraspecific effects (α_{22}) exceed interspecific effects (α_{12}). When these
11 terms are equal, the stabilization term equals one (it drops out); as the degree to which α_{22}
12 exceeds α_{12} increases, stabilization grows increasingly positive. How large the stabilization term
13 must be for coexistence depends on the fitness inequality of the two species. If the fitnesses are
14 close to equal, only weak stabilization is required for coexistence. But as fitness differences
15 increase, a larger stabilization term is required to generate coexistence (Fig. 2).

16

17

1 **Figure Legends**

2 **Fig. 1.** A negative slope in the relationship between per capita population growth rates and a
 3 species' relative frequency in a community (black lines) show the degree of stabilization (niche
 4 differences) in a system. The difference between each species' per capita population growth rate
 5 and zero in the absence of stabilization (gray lines) shows fitness inequality. Neutrality increases
 6 as fitness inequality decreases. The solid and dashed lines refer to two different hypothetical
 7 species.

8
 9 **Fig. 2.** As equivalence in species' average fitness increases, the strength of stabilization
 10 necessary for long-term coexistence decreases. This relationship is illustrated in the following
 11 special case of a two species annual plant competition model (Box 1). We assume symmetric
 12 interspecific competition ($\alpha_{ij}=\alpha_{ji}$) and fixed intraspecific competition ($\alpha_{ii}=\alpha_{jj}=1$) for illustrative
 13 purposes only. The y-axis shows the ratio $\frac{\lambda_1}{\lambda_2}$, the fitness equivalence term for our specific
 14 model (Box 1). When $\lambda_2 > \lambda_1$, as in the figure, coexistence is possible when species 1 can

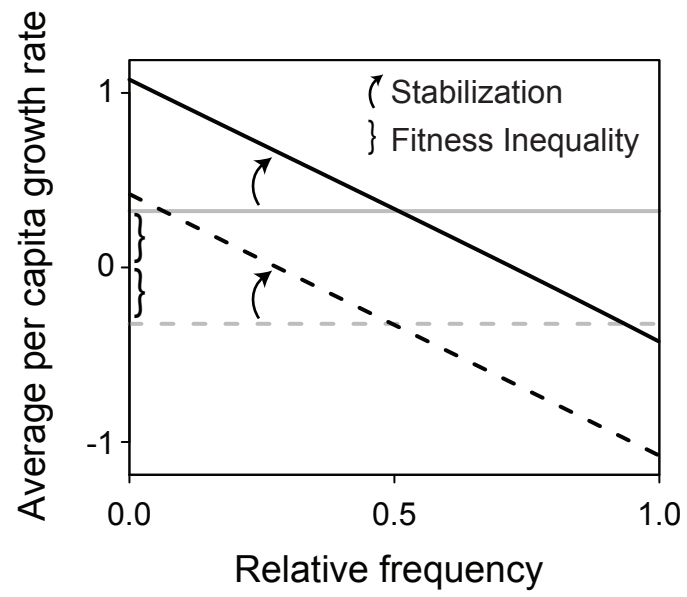
15 increase when rare, which depends on the strength of stabilization, $\frac{\lambda_2}{1 + \left(\frac{\alpha_{12}}{\alpha_{22}}\right)(\lambda_2 - 1)}$ (Box 1).

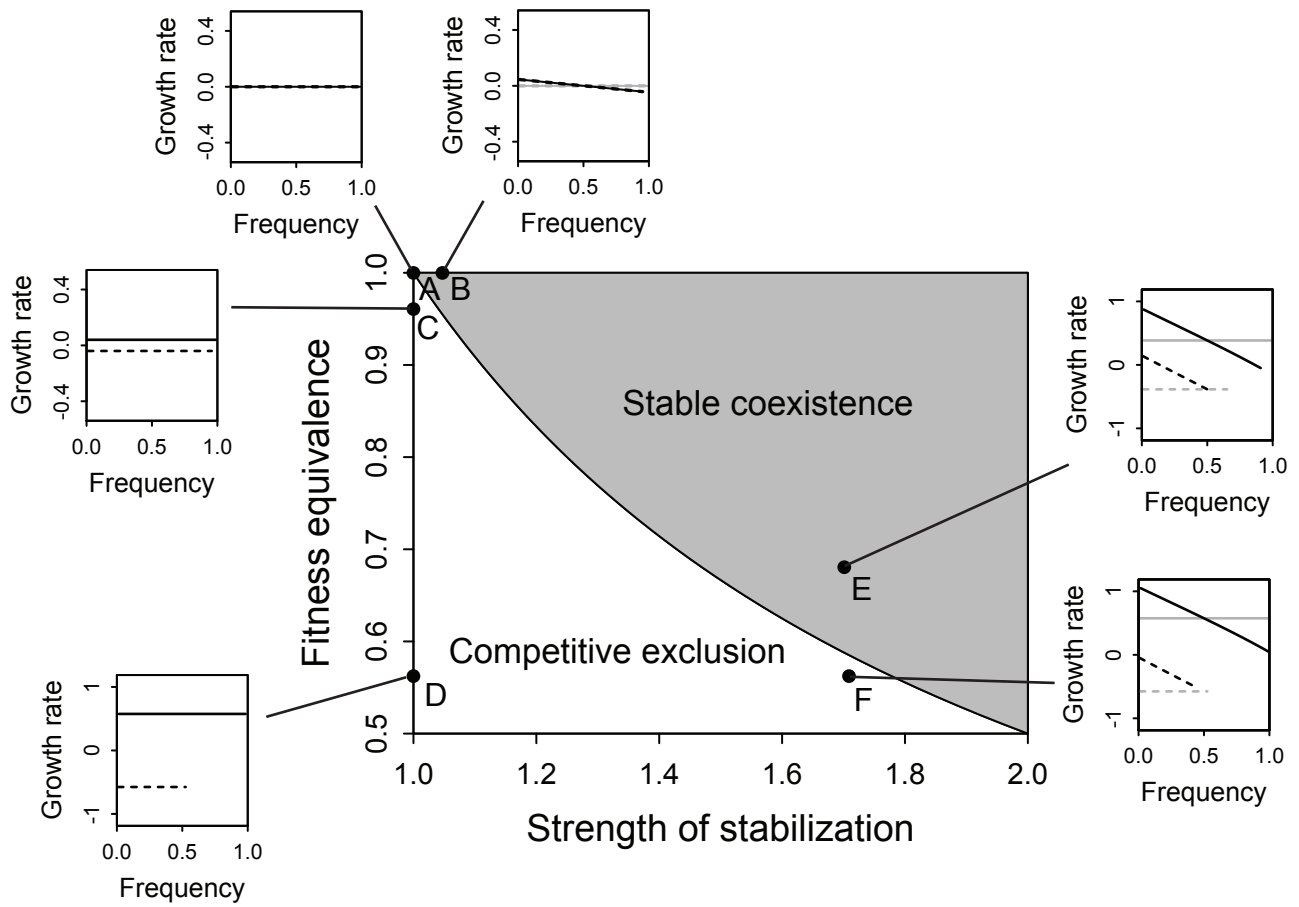
16 This term is shown on the x-axis, and is a function of the degree to which species effect
 17 themselves versus others, $\frac{\alpha_{12}}{\alpha_{22}}$. In the small panels, the black lines show the per capita
 18 population growth rates of the two competing species as a function of their relative frequency in
 19 the community. To generate these curves, we used equations 1 and 2 to calculate the per capita
 20 population growth rate of our target species at densities ranging from near zero to its single

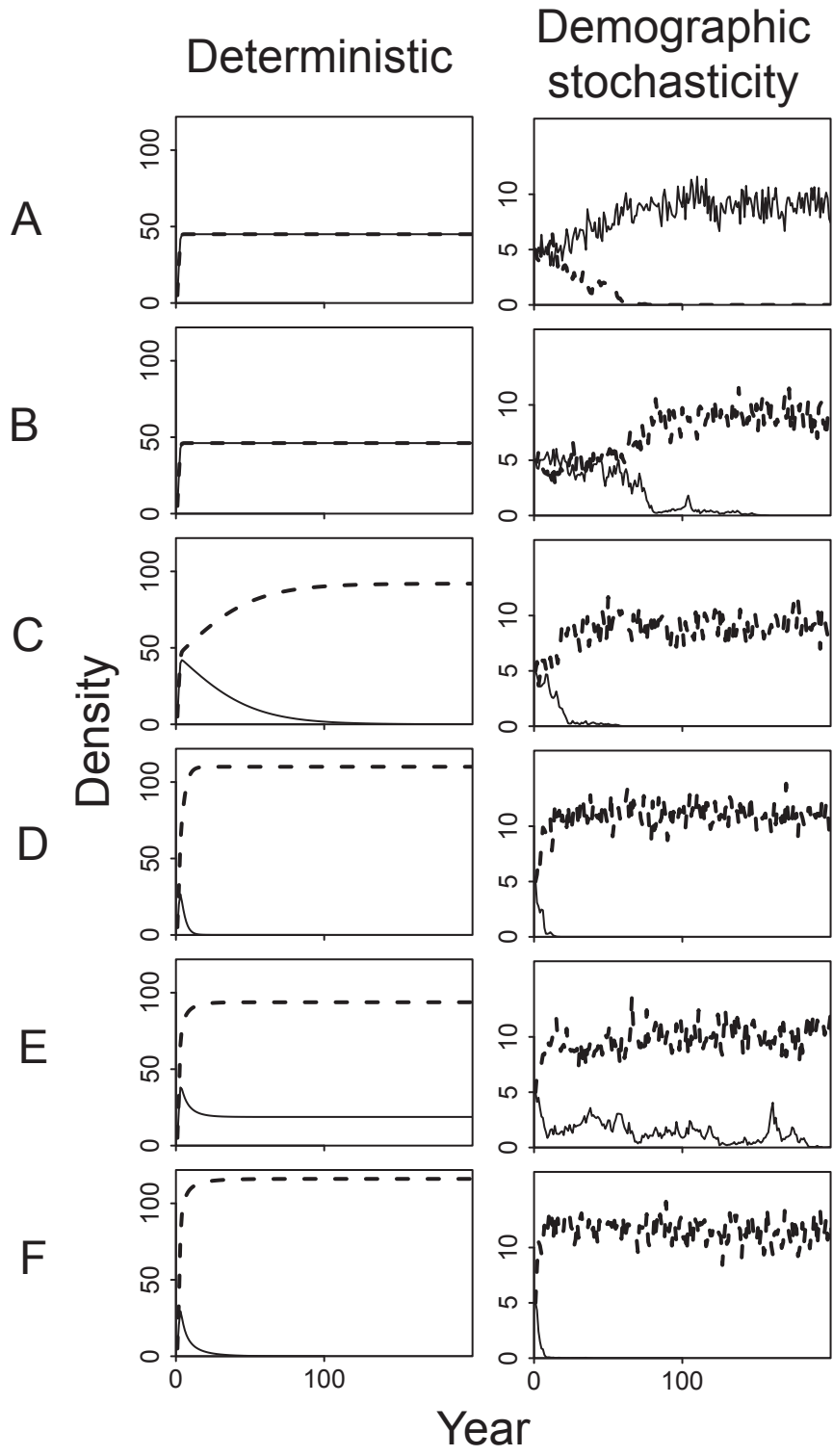
1 species carrying capacity. At each point along this gradient, we set the competitor species at its
 2 equilibrium density given the abundance of the target species, guaranteeing a fully saturated
 3 community. This explains why inferior competitors are never examined at 100% frequency.
 4 Finally, we converted densities to relative frequencies for the x-axis. The grey lines show the
 5 degree of fitness inequality. For A-F, parameter values for $\lambda_1, \lambda_2, \alpha_{12} = \alpha_{21}$ are A: 10, 10, 1; B:
 6 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,
 7 $\alpha_{11} = \alpha_{22} = 1$.

8
 9 **Fig. 3.** Simulated dynamics of two competing species depend on the strength of fitness
 10 equivalence and stabilization (shown by points A-F), but also on demographic stochasticity.
 11 Scenarios A-F refer to labels in Fig. 2, and corresponding parameters are listed in its legend. The
 12 first column of figures is based on simulations of the deterministic model described in Box 1.
 13 The second column adds demographic stochasticity to these simulations by assuming that the λ 's
 14 at each time step follow a Poisson distribution (we assume the λ 's are integers).

15
 16 **Fig. 4.** Three analyses for testing the relative role of stabilizing mechanisms and fitness
 17 equivalence in structuring natural communities. Experimental manipulations or monitoring
 18 combined with simulation models could be used for each of the three analyses. Each analysis
 19 allows increasingly stronger conclusions about the relative importance of stabilizing mechanisms

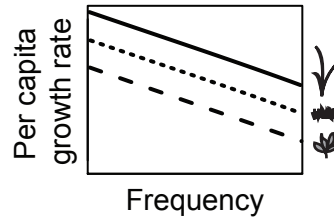




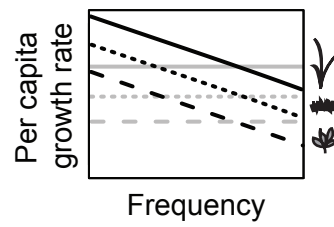


Analyses

1. Quantify stabilization



2. Compare stabilization to fitness inequality



3. Remove stabilization to test its importance for coexistence

