

IDEA AND PERSPECTIVE

Resolving the biodiversity paradox

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Abstract

The paradox of biodiversity involves three elements, (i) mathematical models predict that species must differ in specific ways in order to coexist as stable ecological communities, (ii) such differences are difficult to identify, yet (iii) there is widespread evidence of stability in natural communities. Debate has centred on two views. The first explanation involves tradeoffs along a small number of axes, including ‘colonization-competition’, resource competition (light, water, nitrogen for plants, including the ‘successional niche’), and life history (e.g. high-light growth vs. low-light survival and few large vs. many small seeds). The second view is neutrality, which assumes that species differences do not contribute to dynamics. Clark *et al.* (2004) presented a third explanation, that coexistence is inherently high dimensional, but still depends on species differences. We demonstrate that neither traditional low-dimensional tradeoffs nor neutrality can resolve the biodiversity paradox, in part by showing that they do not properly interpret stochasticity in statistical and in theoretical models. Unless sample sizes are small, traditional data modelling assures that species will appear different in a few dimensions, but those differences will rarely predict coexistence when parameter estimates are plugged into theoretical models. Contrary to standard interpretations, neutral models do not imply functional equivalence, but rather subsume species differences in stochastic terms. New hierarchical modelling techniques for inference reveal high-dimensional differences among species that can be quantified with random individual and temporal effects (RITES), i.e. process-level variation that results from many causes. We show that this variation is large, and that it stands in for species differences along unobserved dimensions that do contribute to diversity. High dimensional coexistence contrasts with the classical notions of tradeoffs along a few axes, which are often not found in data, and with ‘neutral models’, which mask, rather than eliminate, tradeoffs in stochastic terms. This mechanism can explain coexistence of species that would not occur with simple, low-dimensional tradeoff scenarios.

Keywords

coexistence, hierarchical models, neutral models, stochasticity, tradeoffs.

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‘the prevailing notion is that stochastic forces exist on one end of a continuum while deterministic forces occupy the other. Finding any truth that lies between is the challenge. It’s not niche or neutral...it’s determining the relative importance of the two.’ Gewin (2006)

INTRODUCTION

A half-century since Hutchison’s (1961) ‘Paradox of the Plankton’, the explanation for diversity is widely debated. To obtain stable coexistence in models of competing species,

there must be tradeoffs to insure that the best competitors do not drive others to extinction. This theoretical prediction does not square with the widespread observation that many coexisting species do not appear to possess clear differences (Hubbell 1979, 2001; Clark *et al.* 2003, 2004; Chave 2004). The two- to three-dimensional tradeoffs that are the subject of nearly all theoretical and experimental studies of coexistence mechanisms often fail to emerge in data. On the other hand, species show consistent responses to underlying hydrologic and resource gradients (Whittaker 1967; Pastor *et al.* 1984; Tilman 1988; Cavender-Bares *et al.*

2004; Dijkstra *et al.* 2005), during succession (Bazzaz 1979; Pacala *et al.* 1996; Rees *et al.* 2001), and with climate change (Williams *et al.* 2004). Temperate forest tree populations repeatedly expand from glacial refuges to occupy geographic regions that differ among species (e.g. Prentice *et al.* 1991) and return to previous abundances following disturbance (Clark & McLachlan 2003).

'Neutral theory' is viewed as the alternative explanation for diversity. Species are seen as functionally equivalent, lacking niche differences, with slow drift to extinction offset by speciation (Hubbell 1979, 2001; Bell 2000; Volkov *et al.* 2004). Empirical and model evidence is increasingly taken as intermediate between the two, fostering a growing consensus that there may be a continuum of causation from neutrality to niche separation (e.g. Tilman 2004; Gewin 2006; Gravel *et al.* 2006; Holyoak *et al.* 2006).

Here we argue for a revised perspective on the biodiversity paradox that involves an alternative interpretation of both theory and data. First we show that, contrary to the emerging consensus, while *models* do indeed represent a continuum, there is no evidence for such a continuum in the underlying *causes*. Moreover, the continuum in models is one of knowledge, not cause. The two types of models in the debate are special cases, low-dimensional tradeoffs and neutrality representing zero uncertainty and complete uncertainty, respectively. The confusion results from the ways in which unknowns enter both data models (statistics) and process models (theory). The ease with which coexistence can be obtained or extinction forestalled in some types of neutral models results from tradeoffs imposed by stochastic elements in models. Our alternative explanation for causation lies along a different continuum, one of dimensionality. Recognition of the high-dimensionality of coexistence is importantly different from the neutral interpretation, because it implies that 'sameness' is not the alternative to 'lack of difference', when those differences are evaluated along a few observable axes (and they can only be evaluated along a few observable axes). The more appropriate alternative to lack of difference is more dimensions. Because of the high dimensionality of nature (Frank & Amarasekare 1998; Levin 1998; Kneitel & Chase 2003; Clark & Gelfand 2006), we cannot expect to observe many of the forces that structure communities. Moreover, high dimensionality is consistent with the observation of substantial stability in nature, whereas sameness is not. Our claim that high-dimensionality is not appreciated by ecologists might seem at odds with recognition of messy data and complex interactions in the ecological literature. In the Synthesis section of this paper we point out how its role in biodiversity continues to be overlooked in favour of low-dimensional alternatives, the niche/neutralism continuum being the most recent.

Second, we show that traditional treatment of data has contributed to the confusion, and we argue that hierarchical modelling provides an alternative. By ignoring process-level variation, 'statistical models' can suggest strong deterministic differences between species, but not necessarily those differences that would promote coexistence (e.g. tradeoffs). Hierarchical models allow for complexity, by decomposing interactions and structure into manageable units that can be analysed with appropriate computation (Clark 2005; Clark & Gelfand 2006). They accommodate high dimensionality at the process stage, in the form of random individual and temporal effects (RITEs). RITEs represent heterogeneity that results from unknown causes. Moreover, by allowing for inference on hidden variables, we demonstrate that RITEs can indeed stand in for tradeoffs that promote coexistence. By providing a coherent treatment of unknowns from data to prediction, aided by hierarchical modelling, we suggest a resolution to the biodiversity paradox, showing why it may contribute more to stabilizing biodiversity than traditional explanations, and why it can be overlooked.

Our revised view of the biodiversity paradox is organized in four sections. First, we highlight the contradictory implications of theory and data. Subsequent sections each address a critical element of the resolution to this paradox. In the second section, we demonstrate how stochastic process models cannot be used to evaluate the implications of sameness, because they introduce species differences. Third, we discuss how traditional statistical models can imply 'significant' differences among species, but typically not ones that would allow for coexistence in models. These confusing results come in large part from implicit treatment of unknowns. The need for consistent treatment of unknowns in both inference and prediction motivates hierarchical modelling. In the fourth section, we demonstrate how process-level variation can be included in hierarchical models, how it is carried forward to evaluate model behaviour, and how it stands in for underlying (unobserved) species differences.

WHY BIODIVERSITY PRESENTS A —PARADOX

Models of diversity, be they experimental or mathematical, are low dimensional, because (i) they must be tractable, (ii) only a few resources are perceived to be limiting in many communities (e.g. light, water, nitrogen for plants), and (iii) general mechanisms (ones that apply broadly) are believed to be simple, examples being the successional niche (SN), colonization-competition (CC), the storage effect (SE), and tradeoffs involving physiology and/or life history (e.g. Rees *et al.* 2001). Typically, tradeoffs along two or three dimensions are considered in models, experiments and observational studies, rarely as many as five (e.g. Pacala *et al.* 1996;

Wright *et al.* 2006). The tradeoff axes can be two or three life history traits, such as birth rate vs. mortality rate (Warner & Chesson 1985), mortality risk vs. growth rate (Condit *et al.* 2006), high-light growth vs. low-light survivorship (Kobe *et al.* 1995; Walters & Reich 1996), perhaps including mean dispersal distance (Pacala *et al.* 1996), or seed size vs. seed number (Rees *et al.* 2001; Levine & Rees 2002). They can be competitive abilities for resources (Tilman 1982; Gleason & Tilman 1990) or a combination of life history and competition (Tilman 1994; Bonsall *et al.* 2004).

Stable coexistence in models demands that tradeoffs are precisely related, in the form of a precise ordering of parameter combinations. For example, the resource ratio model of Tilman (1982) admits only two coexisting species on two resources at equilibrium and does so only if each consumes more of the resource that limits its own growth rate. With fluctuating resources, we could conceive of multiple coexisting species, but restrictions are still severe: the covariation between resources must be negative, the minimum resource levels needed to sustain the population must trade off precisely, and the consumption vectors for the two resources and minimal resource requirements must be precisely arranged. In models involving tradeoffs between life history and competitive ability high diversity requires a precise negative ordering of competitive abilities and colonization rates (Tilman 1994; Bonsall *et al.* 2004). To raise the bar further, models predict limiting similarity (Pacala & Tilman 1994). Thus, even if the precise ordering of relationships did exist in nature, models additionally require separation of species along these axes.

Field studies often reveal some evidence of tradeoffs (e.g. Wright *et al.* 2006), but not approaching the model requirements for high diversity. Of course, where tradeoffs are present they contribute to diversity. For example, well-understood differences between early- and late-successional species are consistent with SN and CC models (Tilman 1988; Pacala *et al.* 1996; Chesson 2000). Still, many species live together without apparent tradeoffs (Bell 2000; Hubbell 2001; Ricklefs 2003). Whereas niche differences explain why early successional species coexist with late successional species and why species sort out along hydrologic gradients, they do not tell us why dozens of late-successional species coexist, with no obvious niche separation (Chave 2004). The negative correlations tend to be weak or missing and involve, at most, a few axes. Instead of limiting similarity, there is broad overlap (Clark *et al.* 2003, 2004). For example, Condit *et al.* (2006) did not even find that the ranges of growth and mortality rates increase with diversity, as might be expected from the limiting similarity demanded by models.

The apparent lack of tradeoffs presents a paradox when taken in light of the fact that dynamics involving the same

species are not neutral—abundances of many species do not demonstrably ‘drift’ (Clark & McLachlan 2003). Temperate tree populations rapidly expand to similar abundances following glaciations in North America and Europe, they subsequently show decreasing variation among sites over time and, following widespread decimation, return to similar abundances (e.g. the hemlock decline of 5000 year BP). Rather than slow drift, the fossil record shows that coherent spatiotemporal patterns with respect to soils, climate and disturbance sort out rapidly, often within a generation.

To demonstrate why neutral models neither assume functional equivalence nor predict the observed patterns requires a closer look at implied assumptions. Exposing these assumptions represents an important step toward resolving the biodiversity paradox.

INTERPRETATION OF PREDICTIVE MODELLING AND ANALYSIS

Evidence in favour of neutral dynamics is interpreted from patterns of distribution and abundance that are consistent with a neutral model and from empirical studies that fail to find tradeoffs among species (Hubbell 1979, 2001). Here we address the models themselves, and demonstrate that such models do not imply functional equivalence. The treatment of empirical evidence is addressed in the next section.

Neutral models hide tradeoffs

Neutral models do not represent an alternative to tradeoffs. Instead, they relate to knowledge. The confusion comes from interpreting differences based on parameter values that enter stochastic models. For sake of discussion, let x be a predictor, and y a response. As background to the discussion that follows, we let M_s represent a ‘statistical model’, which takes data (x, y) as inputs and produces parameter estimates (β) as outputs, and M_p represent a ‘process model’ that does the opposite: M_p takes parameter estimates as inputs and produces predictions of data (y'), and thus model behaviour, as outputs (Clark 2007). To apply M_s we assume that (x, y) are known (they are observed), and β are unknown (they are represented by estimates—next section). Now if $y_{k,t}$ is a vital rate for species k at time t , and it is drawn from a distribution having parameters β_k , it is not correct to say that species having the same parameter values $\beta_1 = \beta_2$ are indeed the same. They are the same if the outputs are the same, $y_{1,t} = y_{2,t}$. The stochasticity stands in for all of the ways in which $y_{1,t}$ and $y_{2,t}$ differ.

As a specific example, let β_k be a mortality risk for two species having identical estimates of $\beta_1 = \beta_2 = 0.5$. These estimates are outputs of M_s and inputs to M_p . Estimates for the two species could be the same, despite the fact that one dies from starvation and the other from disease, both of

which are unobserved. The estimates of 0.5 reflect the susceptibility of both species to both risk factors and the prevalence of those factors in the sample populations (Clark 2003). Consider the case of ‘maximum stochasticity’ corresponding to estimates of $\beta_k = 0.5$ and quantified by the variance $0.5^2 = 0.25$. When these parameter values are plugged into M_p , the behaviour may or may not be realistic, depending on the differential susceptibilities to these risks, the ways in which these risks covary (is disease more likely where there is starvation?), and on whether or not the random draws of outcomes from the joint density contained in the M_p ,

$$y_{1,t}, y_{2,t} \sim p(\beta_1, \beta_2) \quad (1)$$

capture this covariance structure. There are two important consequences of stochasticity. On the one hand, species parameterized with the same values in M_p are actually different in nature. On the other hand, plugging the same parameter values in M_p causes the species to respond differently (depending, in part, on how we construct $p[\beta_1, \beta_2]$) even if they are the same in nature. We elaborate on this second point in the next section.

First, consider that additional knowledge would allow us to model these risks deterministically. Then M_s would be larger (higher dimensional), having more inputs x and additional parameters associated with each risk. M_s would be more deterministic, it would explain more of the variation, and stochasticity would be reduced. Suppose species 1 has an estimate of 0.05 when disease risk is low and 0.9 when disease risk is high. Rather than the maximum uncertainty associated with the same risks when they are hidden, i.e. $0.5^2 = 0.25$, knowledge of the risks reduces uncertainty to variance $0.05(0.95) = 0.0475$ when this known risk is low and $0.9(0.1) = 0.09$ when it is high. Because the second risk factor is also known, uncertainty associated with that risk is also reduced. With increasing knowledge of additional risks we could continue to chip away at the residual uncertainty, represented as a reduction in the variation associated with stochastic elements. The shift from stochastic to deterministic involves knowledge, not cause. The causes in the first example of limited knowledge are not ‘more neutral’, they are ‘more unknown’.

A lottery example

Lottery models are often used to debate neutrality, and they readily demonstrate how the assumption of identical parameter values in an M_p does not mean that the species are the same. Consider a landscape where two species occupy different niches. For simplicity, we refer to them as ‘low-light gaps’ and ‘high-light gaps’. The first species might be more shade tolerant than the second. There might be many other species occupying the background matrix, but,

for simplicity, we focus on these two. Gaps of different light availabilities are created due to mortality, and they are preferentially colonized by the species that is the best competitor for that gap type. As long as some fraction of both gap types continues to become available, both species can persist, regardless of whether the gap-making process is viewed as deterministic or stochastic. This is a niche model, with each species winning where conditions are most favourable (e.g. Hurtt & Pacala 1995).

Contrast this niche model with a ‘neutral’ one, where sites come available as before, but now occupancy of sites is random, with some probability that either species could win the patch. The model could involve drawing at random the recruitment successes for the two species at each time step or drawing an individual from a randomly chosen species. Depending on specific assumptions, the two species might coexist or not.

What is different about the two foregoing models? In fact, there is no reason why the underlying process must differ at all. The difference lies in how the same process is treated in the M_p . Again, that difference is ‘information’. In the first case, we have knowledge of the underlying process. Because we know what allows colonization of a gap (high light or low light), we include it in the deterministic portion of the model. Whether or not the gap-making process is modelled stochastically, the mechanism for coexistence is treated deterministically we assign each gap to the species favoured there. In the second model, we had no information about why sometimes one species obtained the gap and sometimes the other obtained it. We use stochasticity (a coin flip) to stand in for the lack of information on the process.

If the underlying process in the gap example is the same, why is the second model termed ‘neutral’. If we flip a coin with the same underlying parameter value β_k for recruitment success of both species, ecologists view these species as ‘ecologically equivalent’. Such models are termed neutral if they are assigned the same parameter values representing ‘identical vital demographic rates’ (Volkov *et al.* 2005), in this case, identical success probabilities (see also Bell 2000; Gravel *et al.* 2006). In fact, they are not identical, as evidenced by the way in which we have treated the unknowns, i.e. the structure of the model stochasticity. Because we flipped the coin for each species, these random trials are independent. This means that there will be times and places where one species does well, ‘at random’, when the other does poorly, and vice-versa. We have represented eqn 1 as $p(\beta_1, \beta_2) \equiv p(\beta_1)p(\beta_2)$, ignoring the fact that species will have similar niche requirements [i.e. for large values of β_1 and β_2 , $p(\beta_1 | \beta_2) \gg p(\beta_1)$], and both species will compete strongly for the same sites. The zero correlation assumed by the M_p [$p(\beta_1 | \beta_2) = p(\beta_1)$] promotes coexistence, and it is one way in which the hidden tradeoffs can be taken up in

stochastic terms of models. Said another way, these species are not the same—one is often doing well when the other is not.

To understand how this process differs from one that includes RITEs discussed in the next section, we introduce some notation to describe the structure of stochasticity. Let ε represent a random variate in a model, being the stochastic realization that contributes to a M_p of population growth $y_{k,t}$

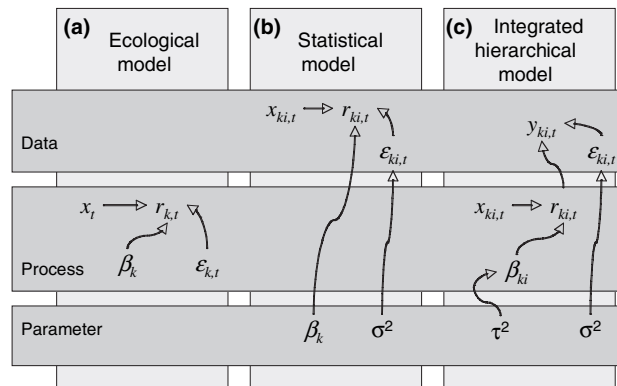
$$y_{k,t} = \mu(x_t; \beta_k) + \varepsilon_{k,t}, \tag{2}$$

where μ is the mean growth rate, which might depend on densities of other species and on the environment, represented by state variables x_t , and responses described by a parameter vector β_k (Fig. 1a). Any stochasticity in this first term is assumed to come from stochastic x_t . Other elements of this term are deterministic. Low dimensional tradeoffs

(e.g. CC and SN) could be taken up by different responses of species, represented here by a different value of β_k for each species. Species with high colonization potential win over those with low potential, unless balanced by a compensatory disadvantage in, say, competitive ability. If $y_{k,t}$ is change in log density, then log-normal stochasticity implies that $\varepsilon_{k,t}$ is the zero-mean process, $\varepsilon_{k,t} \sim N(0, \sigma_k^2)$. The independent variation for each species k implied by this structure insures that species behave differently.

If fluctuations affect both species in a similar way (e.g. drought is bad for both), fluctuations do not necessarily provide an advantage to either. Consider the Gaussian for the joint density in eqn 1,

$$\begin{pmatrix} y_{1t} \\ y_{2t} \end{pmatrix} \sim N \left[\begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix}, \begin{pmatrix} \sigma_1^2 & c\sigma_1\sigma_2 \\ c\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix} \right], \tag{3}$$



(d) HB model of tree demography

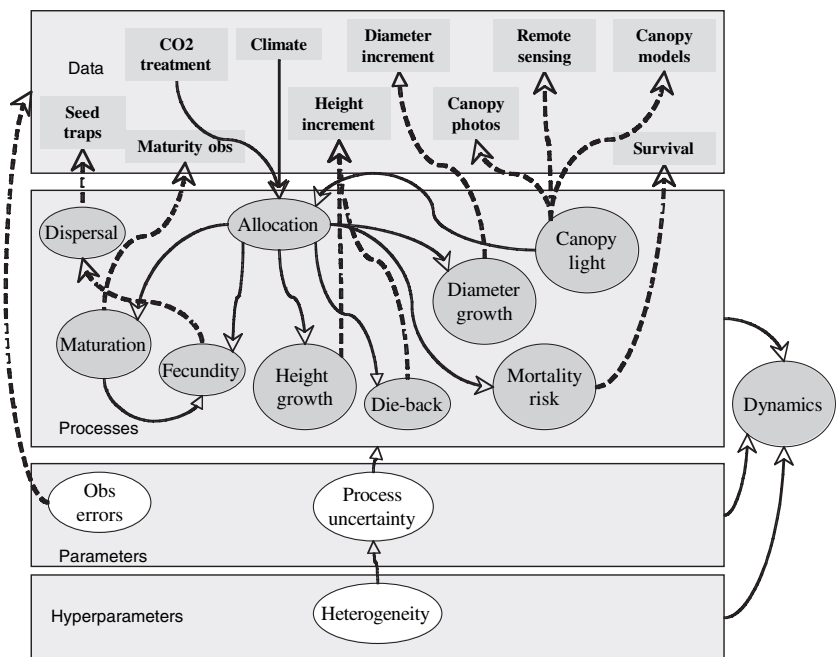


Figure 1 Graphs of models having different structures for stochasticity. Ecological process models (a) focus on process and typically admit independent random variates for each species k and time step t . Traditional statistical models (b) admit stochasticity at the data stage, assuming stochasticity associated with each observation (each time an individual is observed). Hierarchical models (c) have data, process, and parameter stages, admitting uncertainty and variability at all stages. They allow for the complexity in data and processes associated with tree growth, fecundity, and mortality of trees (d). Example estimates from (d) are included in Fig. 4 and described in the Supplementary material.

where c is the correlation between responses of species 1 and species 2. This example does not depend on the assumption of normality, it just simplifies the discussion by allowing us to decouple the means and variances in a one-stage model. Zero correlation in lottery models means that $c = 0$, and we could simply draw independent random variates from $y_{k,t} = N(\beta_k, \sigma_k^2)$, one for each species, at each time step (i.e. $c = 0$ in eqn 2). For complete correlation ($c = 1$) this process simplifies to a single coin flip that applies to both species, $y_{k,t} = \beta_k + \sigma_k \times \varepsilon_t$, where $\varepsilon \sim n(0,1)$ is the zero-mean, unit-variance process. The subscript t indicates that ε_t is drawn once per time step and, thus, applies to both species. Species have different levels of variability (different σ_k), but the absolute correlation assures that neither can exploit the especially favourable situation that might arise if it had a good year while the other had a bad year. With $c = 1$, variability does not promote coexistence, because it does not affect the strength of competition (Chesson 2000). The degree to which species differ depends on the value of $-1 < c < 1$, regardless of β_k . The high correlation that results if we assign the outcome of a single coin flip to both species would represent the underlying lack of ecological differences, the fact that both species require the same recruitment conditions and thus must be exploiting the same types of gaps, the same favourable moisture conditions, and so forth. We do not know what those conditions are, but we can represent them in terms of high correlation. Zero correlation assures species differences.

How important is the distinction identified here between identical parameters vs. identical response? In fact, it is huge. It is *the* reason why it can be easy to obtain coexistence in a lottery M_p , yet so hard to get coexistence in a deterministic version with niche differences, even when multiple dimensions are provided. It can slow the drift to extinction in models that do not predict stable coexistence. The precise parameter relationships needed to obtain coexistence in a niche model are circumvented in a 'neutral model' by assuring low correlation, without saying what the differences are. This is true whether the M_p is analytical, involving analysis of probability distributions, or a numerical simulation.

Not surprisingly, M_p 's having parameter values constructed from a combination of stochastic and deterministic elements (e.g. Tilman 2004, Gravel *et al.* 2006) seem to suggest that coexistence derives from the combination of neutrality and niche differences. There is indeed a combination, but it is a combination of how both deterministic and stochastic elements contribute to species differences. Whether or not species differences are taken up by the deterministic or stochastic components of the model depends on knowledge. Despite identical parameters plugged into a stochastic model, influences that enter between the probability of an event (e.g. birth, growth,

dispersal and death parameter values), which is evaluated on the basis of incomplete knowledge, and the event itself include everything that is unknown about the process, including species differences.

INTERPRETATION OF DATA MODELLING

In view of the fact that there will always be unknowns, models used to understand biodiversity should include stochastic elements. But if simply allowing for unexplained variation in models introduces potential for differences, then how do we develop an understanding of diversity mechanisms that addresses 'important' species differences? We argue that the only operational approach involves assimilation of data, where the different sources of uncertainty are treated as realistically as possible, i.e. at the 'process level' (Clark *et al.* 2004; Clark 2005). Then both knowns and unknowns can be carried forward in models that are directly linked to data. Unfortunately, traditional data modelling tools are not well suited to this task. We point out why and demonstrate why new hierarchical modelling techniques offer an alternative.

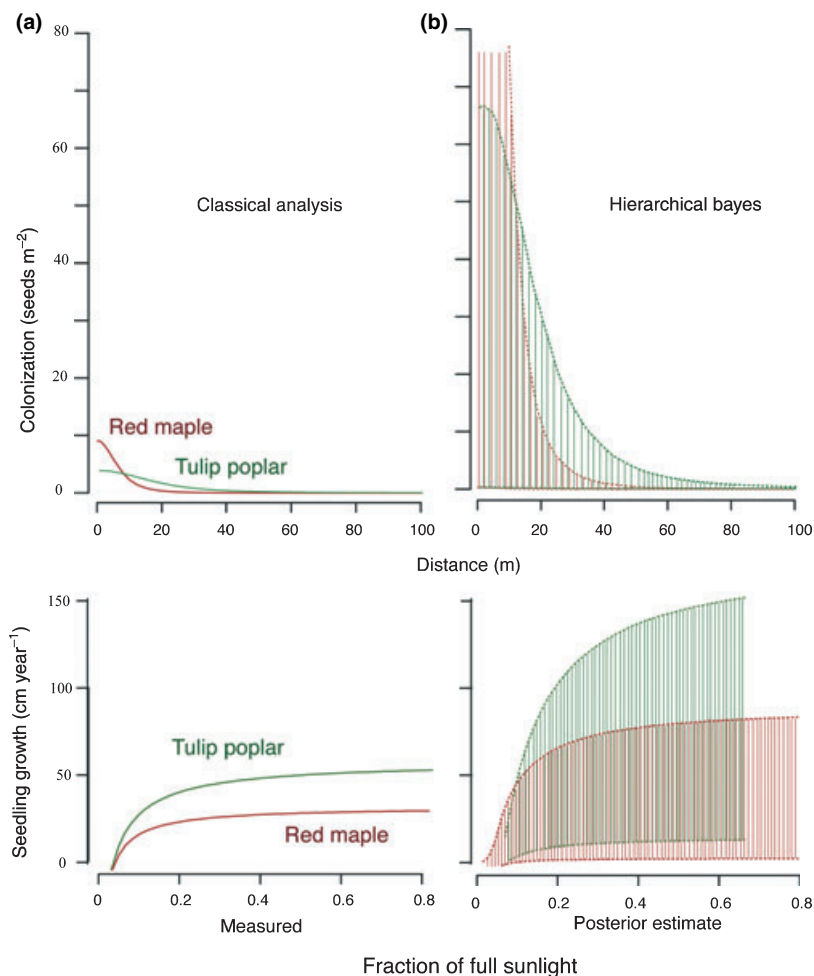
In the foregoing section, we point out that unstated assumptions that enter through stochastic elements can affect model behaviour. Thus, it is imperative to first recognize that the treatment of stochasticity in ecological process models (M_p 's) is, in fact, different from that applied to estimate these relationships (M_s 's). A standard 'statistical model' (M_s) for a data set about the relationship in eqn 2 could look like this:

$$y_{ki,t} = \mu(x_{ki,t}, \beta_k) + \varepsilon_{ki,t} \quad (4)$$

with unknown β_k to be estimated and stochastic $\varepsilon_{ki,t}$ for individual i at time t . The subtle distinction between the M_s (eqn 4) and M_p (eqn 2) is more important than it appears. The estimate of growth responses using model 4 assumes that each observation departs from the mean, taken over individuals and over time. [There are also i and t subscripts on $x_{ki,t}$ because each response observation $y_{ki,t}$ is paired with an observation of environmental predictor(s).] Equation 4 suggests the concept of 'signal' and 'noise'. Individual variability, if it exists, is treated the same as temporal variability; both enter at the data stage, in the error term (Fig. 2b). Thus, it is not surprising that ecologists discard this noise term, and carry forward the signal for use in M_p 's. By contrast, the vast majority of M_p 's (eqn 2) only allow that the full population varies in time. This variation $\varepsilon_{k,t}$ is not the $\varepsilon_{ki,t}$ stochasticity estimated with a M_s in eqn 4 (Clark *et al.* 2003, 2004).

To add to the confusion, not only are the models traditionally used for analysis (the M_p eqn 2) and inference (the M_s eqn 4) different from each other, they both miss the important variation among individuals. In both models,

Figure 2 Contrasting inference for aspects of colonization (seeds dispersed from parent trees) and competition (growth rates at different availabilities of the limiting resource light) using (a) classical and (b) hierarchical Bayes analysis. Classical approaches focus on point estimates with noise at the data stage; there is no distinction of process-level variation, suggesting that tulip poplar is deterministically the better colonizer and competitor. The broad predictive envelopes in (b) are dominated by individual differences within the population. Clark *et al.* (2004) hypothesized that this heterogeneity harbours high dimensional variation that can promote coexistence along many unmeasured axes.



variation among individuals is restricted to their predictor x . These deterministic differences taken up by x are necessarily low-dimensional, because only those found to be 'significant' will be retained. Taken together, we have traditional M_s 's that only admit low-dimensional, deterministic relationships, with everything else in the data take to be noise, and contrasting M_p 's that assume variation is global, applying identically to the entire population(s).

Neither the M_p (eqn 2) nor the M_s (eqn 4) is consistent with the wide variability in real populations that is packaged in the form of individuals (Clark *et al.* 2003, 2004; Clark 2003). Neither the M_p 's, which draw random variates at each time step, nor the M_s 's, which treat each observation as independent, allow for persistent differences among individuals, beyond being exposed to different levels of x . Ecologists tend to think about populations more like this:

$$Y_{ki,t} = \mu(x_{ki,t}, \beta_k) + \varepsilon_{ki,t} \quad (5)$$

(Figure 1c). With addition of the subscript and stochastic specification of β_{ki} we allow for individual differences that persist over time, in addition to those that can be ascribed to

covariates x . Equation 5 says that the population is heterogeneous, with different fecundities, growth rates and so on.

The heterogeneity admitted by eqn 5 can be accommodated at both the inference stage (M_s) and the prediction stage (M_p). In statistical terminology, eqn 5 has random individual effects, and is most flexibly accommodated with a hierarchical M_s (Clark *et al.* 2003, 2004; Clark 2003). Random individual effects are accommodated at the inference stage using a M_p that follows individuals over time, allowing for the variation among individuals that is not taken up by covariates: a value of β_{ki} is assigned at birth of individual i , say $\beta_{ki} \sim n(0, \tau_k^2)$, which determines the fecundity or growth schedules for that individual thereafter. There are now 'high fecundity' and 'low fecundity' individuals. It is the stochastic specification of β_{ki} that adds an additional stage to the model and makes it hierarchical (Clark 2005).

The implications for inference

What are the implications of the stochastic treatment in equation 5? If only observed along two axes, a traditional M_s

for two forest tree species suggests a deterministic winner and loser, with tulip poplar growing faster at all light levels, and colonizing new sites everywhere except directly below red maple trees (Fig. 2a). We show in the next section that these differences are not ones that should lead to coexistence (there is no ‘tradeoff’), although there are tradeoffs involving survival. The traditional approach to inference that leads to Fig. 2a assumes all variation enters at the data stage (eqn 4). Clark *et al.* (2004) hypothesized that allowing for variation in the underlying process (Fig. 1d) could have dynamic consequences, contributing to coexistence. Using hierarchical Bayes to allow for variability within populations, they estimated RITES, finding species overlap (Fig. 2b), in the sense that each population can have individuals with higher reproductive capacities and competitive ability than individuals of the other species (eqn 4). Random individual effects, estimated as the $\beta_{ki,b}$ allow for population variability that cannot be attributed to deterministic causes, because relationships are not observable, not measurable, or not even identified. They can be genetic, but need not be; heterogeneity results from the large number of unmeasured factors that vary on many scales. They can be as large as the deterministic relationships used to infer species differences. In fact, the evidence suggests that circumstances that could make RITEs important dominate: mean differences among species are swamped by variability within populations that cannot be ascribed to specific causes. The differences among individuals that result in broad overlap on Fig. 2b were hypothesized to result from the high-dimensionality of species differences (Clark *et al.* 2004). After illustrating the dynamic consequences in simulation, we demonstrate that this variation does indeed come from species differences along unobserved axes. First we point out how the structure of stochasticity is just as important for RITEs as it is for other sources of stochasticity.

What random individual effects are not

Random individual effects can be confusing at both the inference and prediction stage. At the inference stage, there is not much point to an M_s with random individual effects where there is a single observation per individual – inference will be dominated by the prior, not the data. Moreover, random individual effects are not estimated for events that occur once during the lifetime, e.g. mortality or germination. In both cases, the random effect is redundant with other model elements, and (barring informative priors) we expect identifiability issues. For the latter, population heterogeneity can be estimated by including covariates or with random effects at the group level (Clark *et al.* 2005; Clark 2007). Both approaches borrow information across the population. Finally, random effects are not used to substitute for fixed effects; there is no reason to ignore information. Random

effects allow for heterogeneity that cannot be linked to observable causes.

Likewise at prediction, including an additional random individual effect in an M_p having a single stochastic stage is redundant with any stochasticity that already enters at that stage. It increases the dispersion at that stage, but it does not have any persistent effect over the life of the individual beyond the stochasticity already present. An example would be to include a random draw for individual recruitment success, when recruitment is already random (e.g. a lottery with individual variation in ‘seed production’ or, equivalently, ‘juvenile survival’). In eqn 5, this would amount to drawing error $\varepsilon_{ki,t}$ and $\beta_{ki,b}$ i.e. both entering the model in the same way. A random individual effect that is distinct from ‘error’ involves traits that persist, such as annual fecundity rates and annual growth rates that stay with an individual throughout its lifetime.

IMPLICATIONS OF PROCESS-LEVEL VARIATION FOR PREDICTION

RITEs have dynamic consequences

Figure 3 illustrates the effect for two identical species using a spatially explicit, individual-based stand simulator described by Govindarajan *et al.* (2004). The two ‘species’ differ only in terms of regeneration. One species has the fecundity schedule, seed viability, seed bank and early seedling growth and survival of red maple (*Acer rubrum*), or ‘red’. The second species has those of tulip poplar (*Liriodendron tulipifera*), or ‘green’. In all other respects, species are identical. Green has

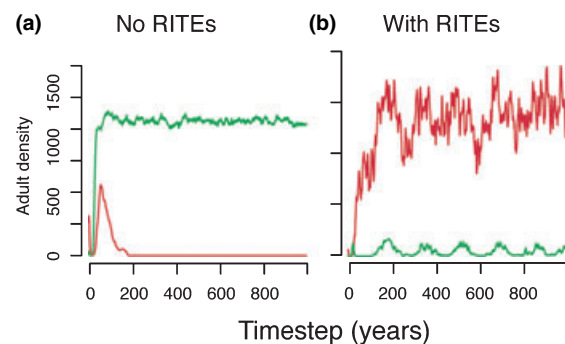


Figure 3 The impact of random individual effects (RITEs) on coexistence of two competing species. Two spatiotemporal and individual-based simulations were run using recruitment processes that are parameterized with data, summarized in Fig. 1. Panel (a) is the traditional approach having deterministic species differences and stochasticity in time, but no within-population heterogeneity, reflecting that fact the green species is the deterministic winner (Fig. 1a). Population heterogeneity in (b) means that green is not the deterministic winner, but rather both species win with some probability.

a strong deterministic advantage due to high fecundity, and it has especially rapid growth. Red has a slight advantage in higher seed bank survival, and higher survival at low light levels (not shown). In this particular simulation, these advantages are not sufficient to save red (Fig. 3a). In simulation, it rapidly goes extinct. Random individual effects admitted in only two short life history stages (Fig. 2b) are enough to stabilize the interaction (Fig. 3b).

Hierarchical modelling identifies underlying differences

Clark *et al.* (2004) emphasize that the spread in Fig. 2b represents underlying high-dimensional variation that can stand in for species differences. The question is, do they in fact represent such differences, and, if so, could they promote diversity? We extended the hierarchical modelling approaches of Clark *et al.* (2003, 2004) to include the full life history and demonstrate that this is the case. At sites in the south-eastern USA, we jointly estimated all demographic rates in response to key environmental variables (Fig. 1D). The hierarchical Bayes model consists of data, process, and parameter stages, assuming that only the data stage can be observed. Although the model contains many parameters and states that are not observable, we can admit far more

information to anchor all parts of the model, because the underlying process is modelled stochastically. The hierarchical treatment allows for full assimilation of information, both theoretical and empirical, at many scales. It allows us to explicitly model variation at the process stage, including species difference that would otherwise be hidden and seem to support the view that coexistence is 'neutral'. A full description of hierarchical modelling is beyond the scope of this paper (Clark 2005, 2007). Here we simply point out examples of the types of unobservable differences that can dramatically influence the perception of species differences (see on-line supplement).

Figure 4 shows large, but hidden differences between the two species from Fig. 2 that will allow each to dominate in different situations. The demographic rates depicted in Fig. 4 are not fitted functional forms, but rather are latent variables, underlying individual traits that are estimated from data as diverse as measurements on small plots, to landscape scale experiments, to remote sensing. None of these relationships are observable, but they can be estimated. For example, the light available to a large tree cannot be measured, but it is related to information that can be obtained from remote sensing, ground observations, and models of solar geometry (M. Wolosin *et al.*, unpublished

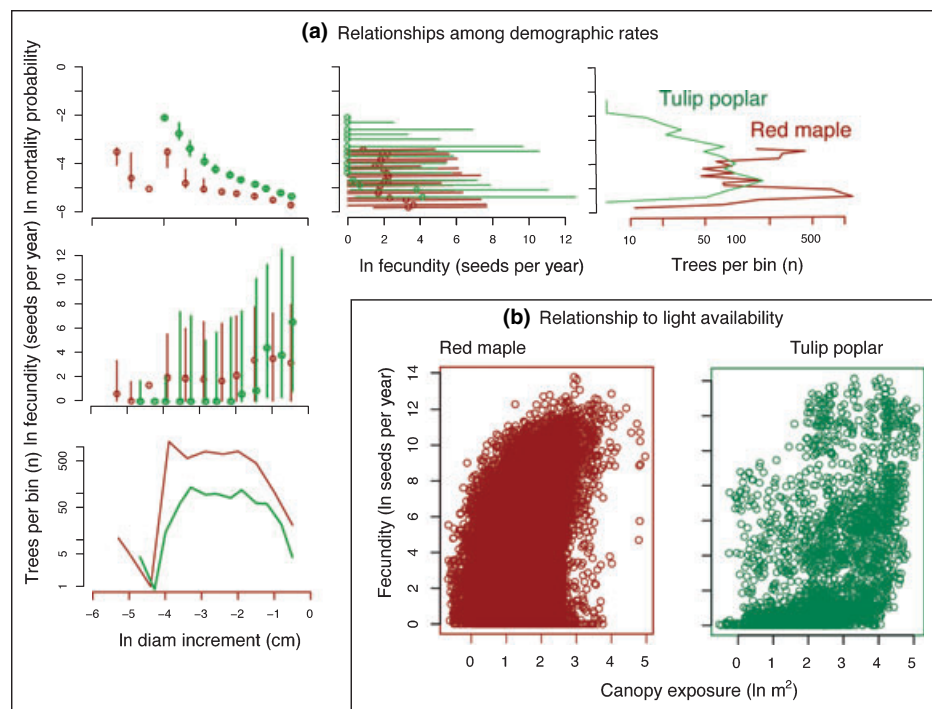


Figure 4 Estimates of state variables from the model in Fig. 1d, showing unobservable differences in species that will allow each the advantage in different settings. Although there are thousands of estimates (Clark *et al.* 2004), there are many different types of information that enter at all scales (Fig. 1d). The estimates reveal that red maple survives better, but produces less seed at low growth rates, whereas tulip poplar does the opposite (a). Red maple produces more seed at low light, and tulip poplar produces more seed at high light (b). None of the state variables shown here are directly observable.

data), and it is embedded within a model that can allow for many known relationships to other variables (Fig. 1d). Estimates for all trees in all years clearly show that red maple has the fecundity advantage in shady sites, while tulip poplar produces more seed with access to more radiation. Likewise, the more rapid increase in mortality risk and decline in fecundity with plant stress, related to diameter growth, are unobservable (Fig. 4b). Tulip poplar has the fecundity advantage at high growth rates, but red maple has the fecundity advantage and an especially strong survival advantage at low growth rates.

We emphasize that realistic correlations in how species respond to the environment does not require fitting the model to all species simultaneously. Although species influence resources in our model, their responses are conditionally independent of one another – if we know the resource level, no new information comes from knowledge of the response of the other species. But marginally, the responses are highly correlated, due to the fact that they are all responding to resources.

In the absence of these estimates ecologists would have no basis for arguing one species or the other has a fecundity advantage, let alone knowing how it shifts with light availability. An ecologist faced with the traditional results of Fig. 2a might say that there are differences, but not tradeoffs. An ecologist confronted with Fig. 2b might say that species overlap and, thus, are the same. As hypothesized by Clark *et al.* (2004), the overlapping intervals of Fig. 2b summarize individual differences in many dimensions. By allowing for process level variation, hierarchical modelling identifies clear differences (Fig. 4). The advantages are capacity to fully exploit information and allowance for unknowns at all stages.

SYNTHESIS

The paradox represented by strict requirements for tradeoffs in models, the difficulty finding enough tradeoffs in data, and the dynamic patterns that implicate stabilizing forces, suggests that a new perspective is needed to understand how species interactions might be stabilized, a mechanism more general than traditional tradeoff arguments and neutrality. We are not the first to suggest that high-dimensionality *might* resolve this paradox (Hutchison 1961). Rather we show that it probably *does* resolve the paradox, showing why other explanations do not, and why this explanation has, for the most part, been ignored.

The stabilizing force represented by high-dimensional variation has been overlooked in both process (theoretical) models and in statistical models. In both cases, the oversight comes from inadequate treatment of stochasticity, but in different ways. On the theoretical side, ‘stochastic regulation’ seems to provide a simple mechanism alternative to

niche differences. Stochasticity can promote coexistence or forestall competitive exclusion in models (Chesson 2000), but it does so by hiding species differences, rather than by removing them. Traditional stochastic process models do not allow for heterogeneity in populations, only fluctuations over time and, more recently, space. Even individual-based models (typically, the most stochastic of ecological models) do not contain random individual effects.

The role of high-dimensionality has also been overlooked when it comes to inference. The traditional practice of applying statistical models with deterministic relationships and residual noise not only ignores process level variation, but it also assures that relationships will appear low dimensional. Simple model selection criteria emphasize parsimony, discarding all effects that do not emerge as significant. Strict application of model selection indices and use of inferential models that lack process-level variation makes species differences appear more important than they are (Clark *et al.* 2003), but these differences will typically not be those that promote coexistence in models. For example, process-level variation is ignored in Fig. 2a. Plugging parameter estimates from this example in to a deterministic process model would assure rapid exclusion, because there is no tradeoff.

The stability conferred by high dimensionality, summarized by RITEs, is distinct from neutral dynamics. There is no evidence to suggest that this overlap is neutral. It is high-dimensional variation resulting from many unmeasured and unmeasurable factors (Clark *et al.* 2004). Neutral models are not ‘tradeoff-free’, they are ‘knowledge-free’. Stochasticity is not an explanation for diversity – it is a way to allow for unknown mechanisms that may or may not promote coexistence. As we increase our knowledge of the process, tradeoffs can emerge (Fig. 4). In models, the structure of stochasticity is critical, but for nonlinear models, effects are rarely generalizable.

If high-dimensionality has been recognized at least since Gleason (1926) and Hutchison (1961), and it is commonly mentioned in reference to the scatter in ecological data, then why do we argue for a reassessment of its consequences for diversity? The emerging consensus that biodiversity maintenance results from a continuum from niche differences to ‘neutral forces’ or ‘stochastic regulation’ may not be the first time ecologists have appealed to a seemingly simple alternative when crude models fail. Despite widespread paleo and contemporary evidence showing populations remaining at relatively constant densities for dozens of generations, responding to climate change in predictable ways, and returning to similar abundances following disturbance, notions of stabilizing forces, such as climax, equilibrium, and niche differences have long been controversial (e.g. Gleason 1926; Whittaker 1953; Botkin 1990). The rejection of stabilizing forces in favour of ‘disequilib-

rium' or 'stochastic regulation' could be the wrong solution to a misidentified problem. Simple models can fail because they omit so many mechanisms that profoundly impact species interactions, regardless of whether or not those models include stabilizing forces. There is a reticence to engage the daunting complexity; the emerging continuum consensus includes no serious discussion of high-dimensional niche differences as the basis for biodiversity maintenance. 'Stochastic regulation' is preferred to high-dimensionality, because it is easier to think about (an apparent one-dimensional alternative to niche differences) and easier to study (coin-flipping in models). Stochasticity seems to be a simple mechanism, approachable by anyone with access to a random number generator. We fully endorse the value of stochastic models, but for a different reason. They do not constitute a new mechanism, but rather substitute for limited knowledge of actual mechanisms. We do not claim that complexity is a new idea in community ecology, only that there are both modelling and empirical reasons why it has not been part of the dialogue.

Neither of our arguments: (i) that 'neutral models' do not assume sameness; and (ii) that high dimensional variation is pervasive, by itself, rules out the neutral hypothesis. However, other observations make it implausible. First, species *are* different, and it would be remarkable if those differences did not confer relative advantages and disadvantages in a high-dimensional world. Second, neutrality is not consistent with widespread stability in nature. Moreover, there is no evidence that coexistence mechanisms lie along a continuum between neutral and niche. This is the case at both the inference and prediction stage. At the inference stage, the broad overlap along observable niche axes (Fig. 2b) is more consistent with higher dimensionality than sameness. At the prediction stage, stochastic models necessarily impart species differences. Because reasonable models must be stochastic (much is unknown), few are appropriate for identifying consequences of sameness.

Then is the neutral model a useful null hypothesis for evaluating the efficacy of niche differences? This is doubtful, because failure to identify differences along observable axes is not evidence in favour of the null of no difference. In a high dimensional world, negative evidence is uninformative.

If not a useful null, perhaps the neutral model adds to understanding in other ways. Possibly, but it may also contribute confusion. For example, the interpretation that limited dispersal distance makes a model 'more neutral' (Gravel *et al.* 2006) is difficult to evaluate. Alternatively, the traditional interpretation of this result, that limited dispersal decreases interspecific competition (most offspring compete with siblings), clearly indicates why competitive exclusion could be slowed (e.g. Neuhauser & Pacala 1999; Holyoak & Loreau 2006). Moreover, the interpretation of causes as a continuum between niche and neutral seems unenlightening.

A niche axis can contribute to coexistence, or not. If it does, we might attempt to quantify it. Whether or not this requires a new continuum view of 'something' vs. 'nothing' is unclear.

The third alternative to traditional niche differences and neutrality, high-dimensional coexistence, is distinct from both and not somewhere between. It joins the observations of species overlap along a few axes with the observation of stability during succession, following glaciations, and along resource and climate gradients. Neither low-dimensional tradeoffs nor neutrality can accommodate these observations. The large variability within populations can stabilize dynamics of species lacking low-dimensional tradeoffs and having, instead, what appear to be broad overlap in responses to resources and life history when considered along only a few axes.

Random individual effects in hierarchical models provide a structure for process-level unknowns that can more appropriately be carried forward in models for prediction and understanding. Such differences result both from genetic variation and from environmental heterogeneity at all scales, from sun flecks to microsites to microclimatic variability, and they involve response scales in space and time. Random individual effects can be stabilizing, because they stand in for high-dimensional variation that persists within populations over time. More importantly, hierarchical models provide for much stronger inference on the hidden processes that do distinguish species (Fig. 4).

The RITE view of biodiversity leads us to draw conclusions that diverge from the mainstream concerning the value of hypothesis tests for species differences. Species are different, and those differences confer advantages and disadvantages in a high-dimensional world. The huge number of trait differences among species (e.g. Marks & Lechowicz 2006) will confer advantages and disadvantages sporadically in space and time (Hutchinson 1961; Frank & Amarasekare 1998; Kneitel & Chase 2003). Proper inferential modelling should recognize them with stochastic elements in stochastic models, but interpret the consequences of model stochasticity appropriately.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Hierarchical model for tree growth, reproduction and survival.

- **Figure S1** Mortality probability estimates for tulip poplar (green) and red maple (red). Lines are posterior means (solid lines) and 95% credible intervals (dashed lines) for

elements of the vectors μ_d (left) and μ_D (right), together with histograms of posterior mean growth rates (left) and diameters (right) for the years preceding death.

- **Table S1** State probabilities for maturation status Q and gender b given observations q .
- **Table S2** Summary of tree and seed data for eight stands and 14 years used in the modelling of Fig. 4. Stands C6, C7, and D were established in 1999.
- **Table S3** Posterior mean and Bayesian standard errors for parameters in the demographic model.

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COMMENTARY ON CLARK *ET AL.* (2007): RESOLVING THE BIODIVERSITY PARADOX

Clark *et al.* take on the dual questions of how not to misidentify neutrality in community ecology, and how to avoid the consequences misidentifying neutrality. These tasks require a clear definition of neutrality. In our view, neutrality is defined by symmetry properties. The basic idea, as epitomized by Hubbell's (2001) models, is that the species identity of an individual does not matter: it has no effect on individual's predicted fate or the fates of its offspring, nor does it have any influence on the fates of others. Crucially, this idea applies simultaneously to any number of individuals from any set of species: all individual-level properties are symmetric with respect to species identity. Most important, models can be symmetric at the species level without being symmetric at the individual level, i.e. without being neutral. For example, consider Lotka-Volterra competition in which all species have the same parameters but intraspecific competition is greater than interspecific competition. Population dynamics would be completely unchanged by permuting the identities of the species. However, this model would not be neutral: an individual's future improves when

it is switched from a species at high density to a species at low density because the reduced intraspecific competition that it experiences is not balanced by the increased interspecific competition. In a neutral model, there is no such effect, because an individual is unaffected by the distinction between conspecifics and heterospecifics. Provided the total number individuals interacting with a given individual does not change, there is no change in its fate.

Species-level symmetry is fully compatible with niche differences that stabilize coexistence, i.e. lead to a tendency for a species to recover from low density whenever it is perturbed there. Of necessity, symmetry at the individual level is lacking (hence neutrality is lacking), because coexistence can only be stabilized if individuals from rare species have consistent advantages (Chesson 1991). Species-level symmetry is sometimes mistaken for neutrality, but in fact is very different. Similarly, Clark *et al.* argue cogently that species stably coexisting might be assumed to have neutral dynamics (and thus not stably coexisting) because they might have similar values for estimates of population parameters. This is especially so when the coexistence mechanism involves vital rates that fluctuate over time. The means of the vital rates might have similar values and give the appearance of