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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 h 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

neutrality, but if the fluctuations involve species differences in responses to their common fluctuating environment, the dynamics are not neutral because individuals of different species respond in different ways. Like Chesson (1986), Clark *et al.* argue that key species differences enabling their coexistence may well reside in these fluctuating vital rates.

In the view of Clark *et al.*, differential responses of species to a fluctuating environment involve high-dimensional tradeoffs between species: therein resides their power for species coexistence. Although a worthy view point, it is not new. In essence, Clark *et al.* advocate the perspective of Grubb's (1977) 'regeneration niche', which has been developed in models as spatial and temporal storage effects (Chesson 2000). Moreover, the presence of the required high-dimensional tradeoffs is amply illustrated by studies of germination in annual plant communities (Adondakis & Venable 2004; Facelli *et al.* 2005). However, there are hazards in seeking coexistence in high-dimensional tradeoffs. First is the problem of confusing sampling error for the true species-level variation (something Clark *et al.* might have emphasized) (Sears & Chesson 2007). Closely related to this issue is the problem of confusing variation between individuals with variation between species. Here, the final claims of Clark *et al.* provide a challenge. They say that phenotypic differences between individuals within species can stabilize coexistence. Such phenotypic differences could in fact be neutral, i.e. not lead to any distinction between heterospecifics and conspecifics, and would therefore be incapable of stabilizing coexistence. How then can we explain Clark *et al.*'s simulation which appears to show coexistence from phenotypic variation?

Clark *et al.* claim phenotypic variation creates temporal variation that has the same effect as species-specific environmentally driven temporal variation. However, this is not the same as between-species tradeoffs. Similar claims of non-species-specific variation standing in for species-specific variation, and stabilizing coexistence (Shorrocks *et al.* 1984; Fagerstrom 1988) have been rebutted in the past (Chesson 1991), based on failure to break individual-level symmetry. A possible explanation of Clark *et al.*'s simulation is an interaction between nonlinearities in the model, of which there are many, and phenotypic variation: when inputs to some nonlinear dynamical process vary over the individuals in a population, the population-level outcome differs from the prediction based on average inputs – Jensen's inequality (Ruel & Ayres 1999; Chesson *et al.* 2005). A plausible outcome is a reduction in average fitness differences between species, making it easier for another mechanism, such as the storage effect, to stabilize coexistence. Phenotypic variation would thus be acting as an equalizing mechanism (*sensu* Chesson 2000), not a provider of stabilizing tradeoffs.

Do neutral models hide tradeoffs as Clark *et al.* claim? In our view, if the neutral models are correct, i.e. satisfy the definition here, they cannot hide tradeoffs between species. Tradeoffs within-species and between-phenotypes are compatible with neutrality: although individuals are not identical, their properties are unaffected by species. Within a neutral model they would not allow stable coexistence, because that is not compatible with neutrality. Species-level symmetry hides tradeoffs, but only if one does not check for individual-level symmetry. Thus, models that depend on species differences in response to a varying environment, e.g. some lottery models, might appear symmetric, especially if the environment were not modelled explicitly, but would not have symmetry at the level of the individual organism. Fitting statistical models that treat essential variation as measurement error, glosses over tradeoffs present in this variation. However, the hierarchical models for data analysis that Clark *et al.* advocate would sharpen understanding of all manner of variation impacting species coexistence, whether by tradeoffs, or by some other means, and result ultimately in much better population models.

Peter Chesson[1] and Mark Rees[2]
[1]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA.*
Email: pchesson@u.arizona.edu
[2]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom.*

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REJOINDER TO CLARK *ET AL.* (2007): RESPONSE TO CHESSON AND REES

Chesson and Rees (C&R) agree with us that ecologists have long recognized complexity (representative citations by us back to Gleason). But their commentary emphasizes that complexity needs more thought. Here we address their objection to simulations that disagree with simple models and their comments on symmetry.

The assumption that simple models extrapolate to complex situations is the basis for much of this commentary. The 'equalizing mechanisms' of C&R come from pioneering work on simple models. These linear equations for population growth have two terms, e.g. one 'environment' and one 'competition' (Chesson & Huntly 1997) or one 'equalizing' and one 'stabilizing' (Chesson 2000). C&R argue that our results are not consonant with simple models, and they suggest a role for variation and nonlinearities. This was our point; nonlinearities combined with stochasticity change behaviour. We seem to agree that nature is complex, but we depart from C&R's low-dimensional focus; even C&R's appeal to Jensen's inequality simplifies variation to a mean and variance. Many processes are 'extreme', tree survival to reproductive age being one obvious example. Means and variances are not enough.

Simple linear equations of population growth omit the processes important in forests. We find no empirical evidence for assumptions that competition and environment can be represented by two terms that, when added together, give population growth rate, that recruitment is inversely proportional to density of competing juveniles (or to a linear transformation thereof – the weighted lottery assumption), that number of species has detectable effects on recruitment success, or that recruitment bears some direct relationship to identities of neighbours. We had to acknowledge seed production, dispersal, seed banks, germination, growth and survival. Each stage is complicated by spatio-temporal variation in weather, soils, pathogens and seed predators, to name just the obvious ones. Species interactions are highly indirect, on many scales. Attempts to shoehorn this process into two additive terms reflect a belief that dimensionality is necessarily low. Simple models based on similar assump-

tions make similar predictions; that does not mean they extrapolate to higher dimensions.

A view that biodiversity maintenance is adequately explained by a few parameters and, perhaps, a coin flip, is at odds with the understanding of high-dimensional systems in many disciplines. In physics, chemistry, genomics and atmospheric sciences, to name a few, sophisticated simulations have become standard research tools, and not because practitioners lack analytical skills. We now know that small changes in assumptions can change behaviour. The familiar Lorenz attractor comes from a seemingly minor third variable that qualitatively changes dynamics. Markov chain Monte Carlo simulations are inherently unpredictable; experience with one application provides limited insight for the next. For many tree species, fecundity explains a 'nonsignificant' fraction of variance in recruitment. Yet, reasonable model behaviour demands its inclusion.

Acknowledging the need for more sophisticated models is not at odds with C&R's laudable emphasis on simplicity. The challenge is recognizing where both can contribute. General circulation models of the atmosphere make predictions that disagree in many ways, but they all get the right answers near an ice sheet. When one or a few forcing variables overwhelm, the dimensionality is effectively reduced. But many of the biodiversity challenges entail a large number of forcings that interact, and none overwhelm. Hierarchical modelling is motivated by the desire for the simplest possible representation. C&R's view that results like ours 'have been rebutted in the past (Chesson 1991)' comes from extrapolation of simple models to situations where there is no reason to expect relevance.

C&R briefly comment on our discussions of data, saying 'there are hazards in seeking coexistence in high dimensional tradeoffs, however. First is the problem of confusing sampling error for the true species-level variation (something Clark *et al.* might have emphasized)'. In fact, we discussed this in detail. The danger C&R suggest is not a serious issue today. On the contrary, current practice in ecology errs in the other direction, overemphasizing one-stage models and formal model selection. Over-reliance on Akaike information criterion (AIC), path analysis and the