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Editor, Nicholas Gotelli
 Manuscript received 19 December 2006
 First decision made 26 January 2007
 Manuscript accepted 29 May 2007

doi: 10.1111/j.1461-0248.2007.01065.x

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

like assures emphasis on simple relationships. Many ecological studies are preoccupied with parsimony to the point where the chosen model defies known causality, because it happens to be the one with the lowest AIC or supported by a path analysis. The danger is actually one of inferring that species are different *in a few dimensions*. One-stage modelling means that all heterogeneity enters at the data stage; there is no hope (or danger) of attributing it to process. Proper interpretation of variation is one of the motivations for multistage modelling, recognizing that unknowns can enter in many ways (Clark 2005, 2007). Our emphasis on RITEs (Random Individual and Temporal Effects) addresses this point.

C&R's comments on 'neutrality' and 'symmetry' are tangential. Their statement about competition (when expressed as simple interaction coefficients) and abundance in the Lotka-Volterra model is correct, but has no direct bearing on model stochasticity. Our point was different, demonstrating that assigning identical parameter values to species in stochastic models does not mean sameness. Once the coin flipping begins, species differ in unspecified ways. The hypothesis that two species or two individuals are the same (or 'symmetric') is logically false, so we move on to the question of whether they might be 'effectively' similar or symmetric? The question could be reasonable to ask only in low-dimensional systems. In a two- or three-dimensional world there could be motivation for the hypothesis of effective symmetry or sameness. When species can and do differ in many ways, we cannot infer symmetry. All we can do is fail to find differences along the few observable axes. The limited information used to test for sameness of species, many never studied beyond a few censuses of growth and survival, would not be enough to show

differences between pre-industrial humans and other primates. C&R's commentary does not challenge our view that the 'niche/neutrality continuum' has become a distraction. At a time with so many biodiversity threats, ecologists need to provide guidance on real processes inferred from challenging data.

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Editor, Nicholas Gotelli

Manuscript received 29 May 2007

Manuscript accepted 29 May 2007

doi: 10.1111/j.1461-0248.2007.01071.x