

**Appendix S1** Minimum value of  $c_{\max}$  for two-species coexistence.

**Appendix S2** Optimal level of preemption for coexistence.

**Figure S1** Optimal level of preemption.

**Figure S2** Rates of change of niche shadows.

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### COMMENTARY ON CALCAGNO *ET AL.* (2006): COEXISTENCE IN A METACOMMUNITY: THE COMPETITION–COLONIZATION TRADE-OFF IS NOT DEAD

Fugitive species persist in the face of superior competitors thanks to a combination of trade-offs (superior colonization or survival ability) and of stochasticity. Models of the competition–colonization–mortality trade-off include several forms of stochasticity, and Calcagno *et al.* (2006) (hereafter CMJD) introduce yet another, that due to pre-emptive effects. Previous studies seem to have ignored the possibility that sites occupied by a competitor might be somewhere between completely available as in the classical models (Hastings 1980; May & Nowak 1994; Tilman 1994) or completely unavailable (Yu & Wilson 2001).

CMJD show that pre-emption favours fugitive species in two ways: (i) reducing the colonization advantage they require to successfully invade superior competitors (the ‘limit to similarity’); and (ii) creating a non-trivial lower limit of the colonization ability superior competitors require to successfully invade them (the ‘limit to dissimilarity’). With perfect pre-emption, the best colonizers win (Yu & Wilson 2001). CMJD demonstrate the counterintuitive result that the interplay between the limits of similarity and dissimilarity can predict maximal diversity at intermediate levels of pre-emption.

This note seeks to clarify the role of stochasticity in this model and to challenge theorists and empiricists to focus on the mechanisms that generate pre-emption. A slight generalization of the CMJD model includes the full competition–colonization–mortality trade-off. The fraction  $p_i$  of sites held by species  $i$ , with colonization rate  $c_i$  and mortality rate  $\mu_i$ , obeys the differential equation

$$\frac{dp_i}{dt} = \left[ c_i \left( 1 - \sum_{j \in \mathcal{S}} p_j \right) - \mu_i + \gamma c_i \sum_{j \in \mathcal{S}} \eta_{i,j} p_j - \gamma \sum_{j \in \mathcal{S}} c_j \eta_{j,i} p_j \right] p_i. \quad (1)$$

The first term tracks colonization of empty sites, the second term tracks mortality, and the third and fourth terms describe sites gained from or lost to species  $j$ , where

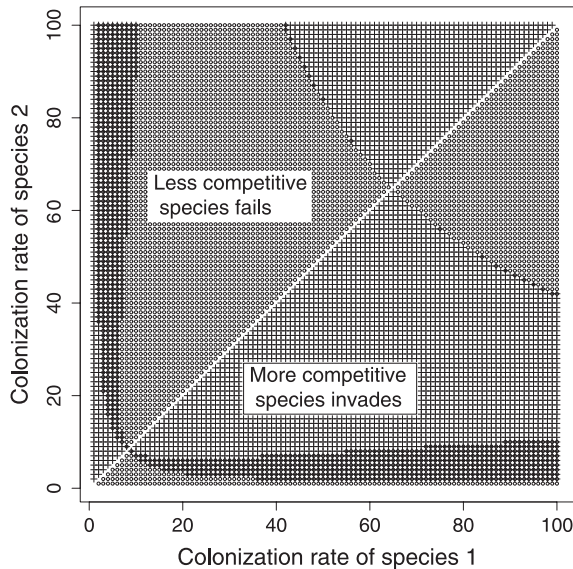
$\eta_{i,j}$  gives the probability the species  $i$  grabs a site from species  $j$ , and  $\gamma$  describes the strength of the pre-emptive effect. The pool of available species is given by the set  $\mathcal{S}$ . Although this model is deterministic, it incorporates at least five forms of stochasticity, which affect diversity in different ways.

- (1) Stochastic colonization: colonization occurs at a rate, meaning that both empty sites and sites occupied by an inferior competitor are not immediately colonized by a superior competitor. This window of opportunity is necessary for coexistence.
- (2) Stochastic mortality: mortality also occurs at a rate. Stochasticity is not essential for coexistence, however, as individuals could die deterministically at a given age without qualitatively altering the results.
- (3) Stochastic outcomes: the classical model sets  $\eta_{i,j} = 1$  if species  $i$  is more competitive than species  $j$ , and  $\eta_{i,j} = 0$  otherwise. Intermediate, and thus probabilistic, values decrease the degree of coexistence in an uninvadable community (Adler & Mosquera 2000).
- (4) Stochastic pre-emptive effects: CMJD introduce a related phenomenon by scaling the maximum probability of takeover to  $\gamma$ , which can be  $< 1$ .
- (5) Stochastic assembly: the set  $\mathcal{S}$  describes the species pool. Adler & Mosquera (2000) removed this aspect of stochasticity by considering all possible species, while CMJD consider randomly selected subsets.

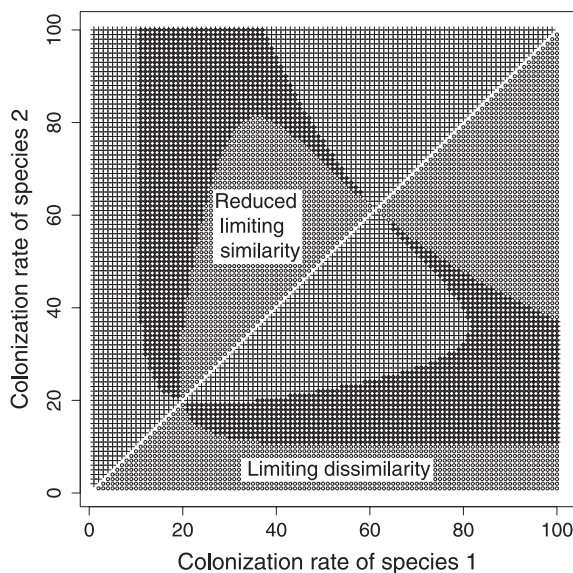
Why do we find all of this stochasticity in a deterministic model? In the context of statistics, ‘stochasticity stands in for the unknowns and unmeasurables’ (Clark 2005). Something determines when colonizers appear and whether one species takes over a site from another, but we may not know or care to know the details of wind, timing, and microhabitat that underlie these processes. Including some of the more tractable details of the takeover process, however, could help to unify stochastic outcomes with stochastic pre-emptive effects. Mosquera & Adler (1998) derive related models of host takeover in epidemiological models, showing explicitly how different assumptions about intrahost competition lead to different models of pre-emption and different patterns of coexistence.

The species pool  $S$  is created by the ecological and evolutionary history of a region, and lives firmly in the realm of the unknown. CMJD explore this by sampling in a particular way from a particular subset of possible species. I follow their lead, but illustrate the results in a different way, using pairwise invasibility plots (Geritz *et al.* 1998). Let  $\omega_i$  represent the competitiveness of species  $i$ . Assume a competition–colonization trade-off  $c_i = 1 - 25 \log(\omega_i)$ , a competition–mortality trade-off  $m_i = \omega_i$ , and

$$\gamma = 1$$



$$\gamma = 0.1$$



**Figure 1** A pair of pairwise invasibility plots. Circles show values of the parameters where species 1 can invade species 2, plus represents species 2 can invade species 1, and the overlap is the region of mutual invasibility and coexistence.

$$\eta_{i,j} = \frac{e^{-5\omega_j}}{e^{-5\omega_i} + e^{-5\omega_j}}$$

(functional forms based on combining CMJD with Adler & Mosquera (2000), parameter values chosen using a stochastic selection scheme). Figure 1 shows pairwise invasibility plots comparing  $\gamma = 1$  with  $\gamma = 0.1$ . With  $\gamma = 0.1$ , a more competitive species 2 requires a higher colonization rate to invade (limiting dissimilarity), while a less competitive species 2 can succeed with a lower colonization rate (reduced limiting similarity). If two species were chosen independently and uniformly from these regions, the probability of coexistence is 0.284 when  $\gamma = 0.1$ , and only 0.115 when  $\gamma = 1$ . But there are many ways to choose species, and a method that tends to choose species with low colonization rates would reverse the result.

Given this, should we be surprised that intermediate levels of the pre-emptive effect can lead to increased diversity? The pairwise invasibility plots show that reducing  $\gamma$  leads to coexistence of species with higher colonization rates, and any sampling method that emphasizes these species will generate higher standing diversity. The surprise is that plausible sampling schemes do exist which create this effect.

CMJD challenge theorists and empiricists in at least four ways. First, we should check empirically whether inferior competitors do indeed limit the survival of superior competitors through pre-emption. Second, we must chase down the unknown mechanisms leading to stochasticity in the outcomes of interactions between individuals (Mosquera & Adler 1998). Third, we must work to understand the larger metacommunity from which species are sampled. Fourth, we must decide how empirical measures of diversity relate to different theoretical measures of diversity, such as the number of species in an uninvadable community, the number of species maintained from a random sample, or the probability that all members of a random sample are maintained. Finally, of course, we must ensure that our imaginative space is not pre-empted by pre-conceived notions about these important ideas.

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### REJOINDER TO CALCAGNO *ET AL.* (2006): WHICH IMMIGRATION POLICY FOR OPTIMAL COEXISTENCE?

Adler (2006) makes some important remarks about our results (Calcagno *et al.* 2006, hereafter CMJD). He nicely illustrates the effect of preemption on the limits to similarity and dissimilarity, by plotting, within the square defined by all pairs of species, the area in which coexistence is possible. Note that the ratio of this area over the total surface of the square is the probability of two-species coexistence ( $p_2$ ) we defined. Adler uses the general form of our model, in which the extinction rate  $\mu$  is not constant across species and is also in trade-off with competitiveness (Tilman 1994). We shall mention that, interestingly, a trade-off between survival and competition does not induce a positive effect of preemption on coexistence *per se*, only the competition–colonization (CC) trade-off is responsible for that (V. Calcagno, unpublished results).

Most importantly, Adler points out that our results are obtained by drawing colonization rates from a uniform distribution on  $(\mu, c_{\max}]$ , with  $c_{\max}$  the maximum achievable colonization rate. Clearly, the uniform distribution has no canonic value in this case: we have no idea of what would be the distribution in natural communities. Many probability distributions for colonization rates of immigrant species could arguably be used, and resulting probabilities of coexistence would differ. This is an unavoidable problem when dealing with ‘randomness’ on continuous variables: we cannot avoid specifying an arbitrary prior distribution. In epistemology, this is classically known as Bertrand’s paradox, after the French mathematician Joseph Bertrand (1888).

To cope with this, it is of course possible to consider several probability distributions of immigrant colonization

rates (it is what May & Nowak 1994 did), but clearly one cannot hope to explore all possible distributions. Fortunately, from our results we can figure out what any specific distribution for species colonization rates would imply for the probabilities of coexistence. The value of  $p_2$  as a function of  $c_{\max}$  (Fig. 3b in CMJD) illustrates the ‘density’ of coexistence for different colonization rates. It clearly shows that coexistence is more likely for small colonization rates, except very small ones when  $\alpha$  is finite. Similarly, the effect of preemption for various  $c_{\max}$  (Fig. 5 in CMJD) indicates that preemption is more beneficial for high colonization rates. Thus, we can intuitively conclude that any probability distribution giving more weight to small (large) colonization rates is expected to favour (disfavour) coexistence, and to weaken (strengthen) the positive effect of preemption.

To illustrate this, let us consider two widely used distributions: the exponential and the log-normal. Note that both of these distributions (especially the exponential) emphasize low colonization rates (Fig. 1a,c). A very general argument of the kind ‘best colonizers get there first’ [formally meaning that there is a positive correlation between the (within metacommunity) colonization rates and the (between metacommunities) immigration rates] would lead to the reverse situation: high colonization rates would be over-represented within immigrants, and this would reinforce the positive role of preemption on coexistence. We thus use these two distributions as worst-case scenarios.

The general form of eqn 8 in CMJD, for any distribution of colonization rates with density  $f(c)$  and cumulated probability  $F(c)$  on  $(\mu, \infty)$ , is

$$p_2(\theta) = 2 \int_{\mu}^{\infty} f(c_2)(F(c_r) - F(c_D))dc_2. \quad (1)$$

Results are shown in Fig. 1. As expected, preemption is less