Clark, J.S. (2005). Why environmental scientists are becoming Bayesians. *Ecol. Lett.*, 8, 2–14.

Geritz, S.A.H., Kisdi, E., Meszena, E. & Metz, J.A.J. (1998). Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, 12, 35–57.

Hastings, A. (1980). Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.*, 18, 363–373.

May, R.M. & Nowak, M.A. (1994). Superinfection, metapopulation dynamics, and the evolution of diversity. *J. Theor. Biol.*, 170, 95–114.

Mosquera, J. & Adler, F.R. (1998). Evolution of virulence: a unified framework for coinfection and superinfection. *J. Theor. Biol.*, 195, 293–313.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.

Yu, D.W. & Wilson, H.B. (2001). The competition-colonization trade-off is dead; long live the competition-colonization trade-off. *Am. Nat.*, 158, 49–63.

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 μ is not constant across species and is also in trade-off with competitivity (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on coexistence *per se*, only the competition–colonization (CC) trade-off is responsible for that (V. Calcagno, unpublished results).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 (μ, 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).

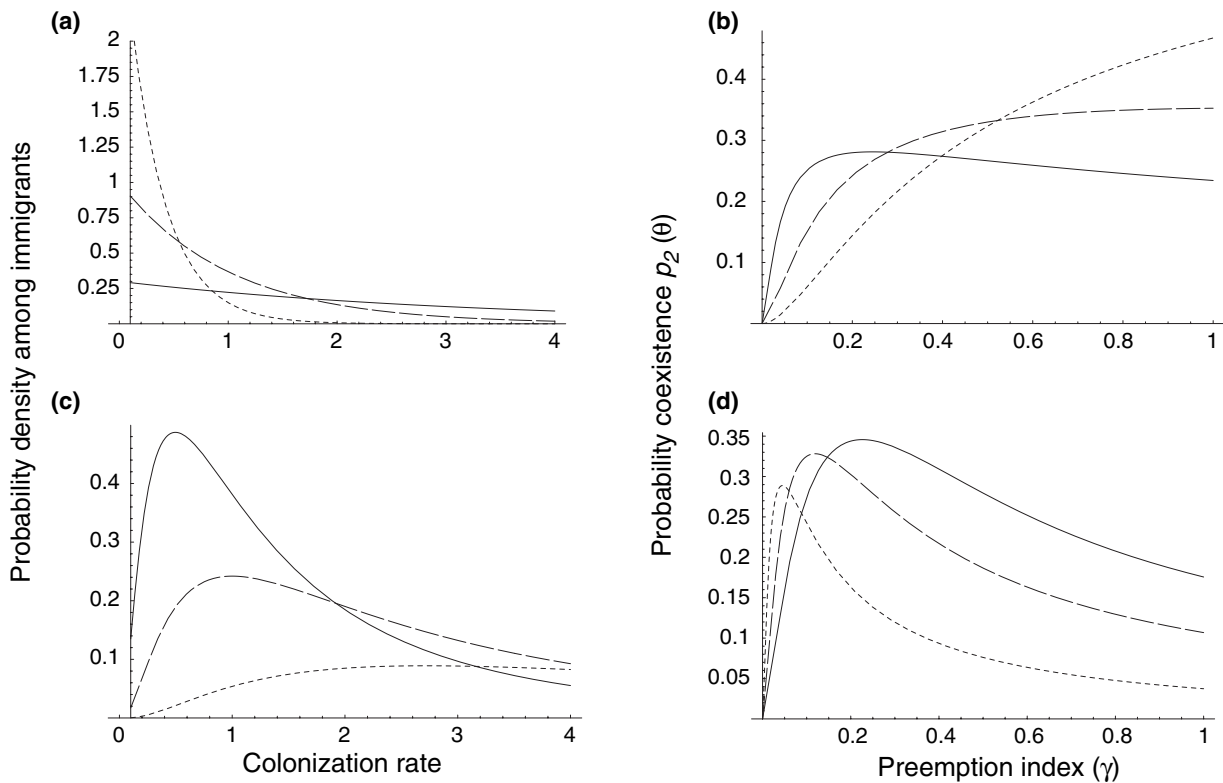To cope with this, it is of course possible to consider several probability distributions of immigrant colonization rates (it is what May & Nowak 1994 did), but clearly one cannot hope to explore all possible distributions. Fortunately, from our results we can figure out what any specific distribution 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 α 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 (μ,∞), is

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

Results are shown in Fig. 1. As expected, preemption is less
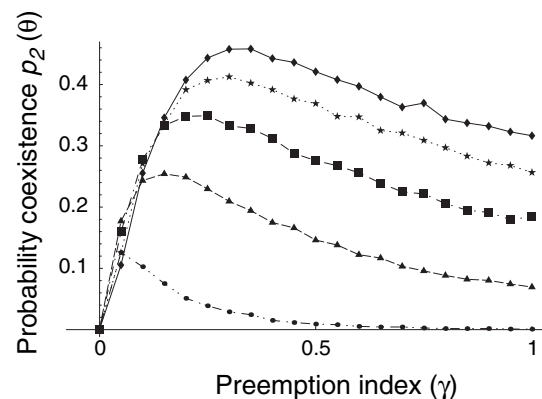
Figure 1 Non-uniform regional pools: effect of preemption for various probability distributions of colonization rates. (a) Exponential distribution. The probability density is plotted for scale parameters 0.3 (continuous line), 1 (dashed line) and 3 (dotted line). Corresponding 50% quantiles are 2.4, 0.8 and 0.3. (b) Effect of preemption for the exponential distributions illustrated in (a). (c) Log-normal distributions. The probability density is plotted for standard deviation parameter 1 and mean parameters 0.3 (continuous line), 1 (dashed line) and 3 (dotted line). Corresponding 50% quantiles are 1.45, 2.8 and 20.2. (d) Effect of preemption for the log-normal disributions illustrated in (c). Numerical integrations of eqn 1. Parameters: $\mu = 0.1$, α infinite.

favourable to coexistence when colonization rates are smaller (see quantiles in the legend of Fig. 1).

Along the same lines, we can relax the assumption of independent immigration of species, and consider instead that the colonization rates are positively (or negatively) correlated. As before, we can conclude that a positive (negative) correlation would make species more similar (different), and thus emphasize the role of the limit to similarity (dissimilarity). As a consequence, a positive correlation should globally make coexistence less likely but strengthen the beneficial effect of preemption. Figure 2 illustrates this, for two species and a joint log-normal distribution of their colonization rates.

Overall, the positive effect of preemption appears to be a robust phenomenon, whatever the precise characteristics of the immigrant regional pool.

More generally, we agree with Adler that deriving the values of the preemption index (γ) and the shape of the trade-off function (η) from underlying biological processes is fundamental. The logistic function we use for η, although

Figure 2 Correlated regional pool: effect of preemption when colonization rates are correlated. Species have colonization rates drawn from a joint log-normal distribution, with standard deviation parameter 1, mean parameter 0.3, and correlations (from bottom to top) +0.9, +0.5, 0, −0.5 and −0.9. The case with zero correlation is equivalent to the case with mean 0.3 in Fig. 1d. Monte Carlo estimations with sample size 10 000. Parameters: $\mu = 0.1$, α infinite.

commonly employed (e.g. Geritz *et al.* 1999; Bonsall *et al.* 2004), is purely arbitrary. Similarly, while in our model preemption and trade-off intensity are independent, they may well be linked as a result of common underlying stochastic processes. In this sense our model of competition is phenomenological, and it is important to understand what values of γ and η specific mechanisms would produce. Mosquera & Adler (1998) made such an effort to derive an analogous of γ from the intrahost dynamics of parasites. More effort is needed to make phenomenological parameters emerge from underlying processes, and this could help unify the various theories of spatial coexistence developed in different fields, especially epidemiology and plant ecology, but also life-history evolution (Olivieri *et al.* 1995).

Vincent Calcagno[1]*, Nicolas Mouquet[1],
Philippe Jarne[2] and Patrice David[2]
[1]*ISEM, University of Montpellier II, Montpellier, France*
[2]*CEFE, CNRS, Montpellier, France*
*E-mail: calcagno@isem.univ-montp2.fr

REFERENCES

Alder, F.R. (2006). Commentary on Calcagno *et al.* (2006): Coexistence in a metacommunity: the competition–colonization trade-off is not dead. *Ecol. Lett.*, 907–909.

Bertrand J. (1888). *Calcul des Probabilités.* Gauthier-Villars, Paris.

Bonsall, M.B., Jansen, V.A.A. & Hassell, M.P. (2004). Life history trade-offs assemble ecological guilds. *Science*, 306, 111–114.

Calcagno, V., Mouquet, N., Jarne, P. & David, P. (2006). Coexistence in a metacommunity: the competition–colonization trade-off is not dead. *Ecol. Lett.*, 897–907.

Geritz, S.A.H., van der Meijden, E. & Metz, J.A.J. (1999). Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Popul. Biol.*, 55, 324–343.

May, R.M. & Nowak, M.A. (1994). Superinfection, metapopulation dynamics, and the evolution of diversity. *J. Theor. Biol.*, 170, 95–114.

Mosquera, J. & Adler, F.R. (1998). Evolution of virulence: a unified framework for coinfection and superinfection. *J. Theor. Biol.*, 195, 293–313.

Olivieri, I., Michalakis, Y. & Gouyon P.H. (1995). Metapopulation genetics and the evolution of dispersal. *Am. Nat.*, 146, 202–228.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.