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IDEA AND PERSPECTIVE

Coexistence in a metacommunity: the competition–colonization trade-off is not dead

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Abstract

The competition–colonization trade-off model is often used to explain the coexistence of species. Yet its applicability has been severely criticized, mainly because the original model assumed a strict competitive hierarchy of species and did not allow for any preemptive effect. We considered the impact of relaxing both of these limitations on coexistence. Relaxing trade-off intensity makes coexistence less likely and introduces a minimum colonization rate below which any coexistence is impossible. Allowing for preemption introduces a limit to dissimilarity between species. Surprisingly, preemption does not impede coexistence as one could presume from previous studies, but can actually increase the likelihood of coexistence. Its effect on coexistence depends on whether or not species in the regional pool are strongly limited in their colonization ability. Preemption is predicted to favour coexistence when: (i) species are not strongly limited in their colonization ability; and (ii) the competitive trade-off is not infinitely intense.

Keywords

Asymmetric, coexistence, colonization, competition, dissimilarity, dominance, preemption, similarity, spatial, trade-off.

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INTRODUCTION

Community ecology aims at explaining biodiversity in terms of mechanisms underlying species coexistence (Chesson 2000). Most models of species coexistence proposed so far differ along the following axes (Chave *et al.* 2002): (i) are species differences responsible for coexistence or are they neutral? (ii) Is the environment heterogeneous? (iii) Is the environment spatially structured? Popular models involving spatially structured landscapes have flourished in the last decade (Amarasekare *et al.* 2004). Spatial processes in an assemblage of local communities connected by dispersal (or metacommunity, Leibold *et al.* 2004) are crucial in these models, although the scale of the spatial structure can vary. The most popular model of this kind is arguably the competition–colonization (CC) trade-off model. It provided the impetus for much theoretical and empirical research, and is commonly used to assess the impact of habitat destruction on biodiversity (Nee & May 1992; Tilman *et al.* 1994; Banks 1997). Incidentally, its applicability spreads well beyond community ecology, as this same model is used to describe the epidemiological dynamics of host–parasite interactions (May & Nowak 1994; Nowak & May 1994).

This model of coexistence relies on the intuitively appealing principle that species that are very good at colonization (e.g. with high fecundity or dispersal) may be poor competitors. The idea can be traced back to Skellam (1951), yet the most popular formalizations are those of Levins & Culver (1971), Hastings (1980), Nee & May (1992) and Tilman (1994). In these patch-occupancy models, local (within-patch) dynamics are assumed to be instantaneous relative to global dynamics (Hanski 1983). Note that the nature of a local 'patch' of habitat may vary. While in epidemiology patches refer to individual hosts, in community ecology, they may be either local populations (Levins & Culver 1971) or 'safe sites' (Geritz *et al.* 1988; Tilman 1994) supporting at most one adult individual. In all cases, patches are connected by dispersal. Further assumptions are: (i) local competition is fully asymmetric, i.e. there is a strict competitive hierarchy and a superior species will always displace, and never be displaced by, a subordinate species; (ii) the outcome of competition is not affected by the resident or migrant status of competing species (a situation known as 'dominance competition' or sometimes as 'displacement competition'). This means that a species occupying a site does not benefit from any preemptive effect, and can be outcompeted all the same. Under these conditions, the model predicts the coexistence of a potentially infinite number of species (Tilman 1994).

There have been several objections to the CC trade-off model and to its potential role in natural communities. The first concern was that stochasticity, with a finite number of sites, would limit the number of coexisting species (Goldwasser *et al.* 1994). More recently, the model has been severely criticized on two grounds: (i) in nature, local competition is rarely fully asymmetric but rather of intermediate form, and (ii) while in the model the outcome of competition is not affected by the migrant status of competing species, in real-life situations it may be hard, or impossible, for a propagule to colonize a site already occupied by a species (i.e. there is some preemption).

Several papers have discussed these two objections. Banks (1997) briefly addressed the consequence of what he calls 'messy' trade-offs for biodiversity loss, but he retained the original assumption of a strict competitive hierarchy. Adler & Mosquera (2000) derived criteria linking the shape of the trade-off function to the number of coexisting species in a related model, but they were looking for invasion-resistant communities only. The role of trade-off intensity on coexistence was later addressed by Levine & Rees (2002), in an effort to use empirical estimates of trade-off parameters. Unfortunately, they used simulations of rather specific annual plant assemblages, making comparisons and broad conclusions difficult. Yu & Wilson (2001) considered pure preemption competition (which they called 'replacement' competition), while retaining the assumption of a strict competitive hierarchy. They restrained themselves to two species, and did not investigate any intermediate between preemption and dominance competition. Their main result is that the model with pure preemption does not allow coexistence, suggesting that coexistence cannot be accounted for by the CC trade-off alone. Kisdi & Geritz (2003a,b) further investigated the coexistence of two species with preemption, introducing a different discrete time model specific to plants with periodic seed release. Their conclusions largely depend on the model structure, which introduces small-scale heterogeneity resulting from demographic stochasticity (Amarasekare 2003; Kisdi & Geritz 2003a,b). Most of these studies were concerned with annual plant communities and the 'safe site' interpretation of the model. Their overall conclusion is that unless local competition is quasi-perfectly asymmetric and not preemptive, the CC trade-off model is unlikely to explain coexistence. Yu & Wilson (2001) even claimed that the CC trade-off was 'dead'.

While the original model was intended to be a general model of community ecology (including parasite dynamics), the objections highlighted above have not been fully discussed for the general CC trade-off model. The aim of this work is to explore the range from dominance to preemptive competition and from perfectly asymmetric to symmetric local competition. We consider the impact of these competition modalities on the possibility for two or more species to coexist. We will show that relaxing the original assumptions of the model is far from 'killing' coexistence. On the contrary, it produces conditions under which coexistence is favoured, rather than prevented.

MODEL AND METHOD

We start with the model of spatial competitive trade-off most widely used in biology, and especially in community ecology (see Hastings 1980; Nee & May 1992; Nowak & May 1994; Tilman 1994). This is the multispecies extension of Levins (1969) model of metapopulation, and we will henceforth refer to it as the Hastings–Tilman (HT) model.

We describe a metacommunity structured in a large number of discrete patches of habitat connected by events of migration and colonization, and subject to random perturbations resulting in local extinctions. The metacommunity is composed of n competing species. Each species i is defined by three quantities: its colonization rate (c_i), its extinction rate (m_i) and its competition index (ω_i). For easier interpretation, we will take $m = \mu$ for all species, where μ reflects the perturbation rate of the environment (Hastings 1980; Kinzig *et al.* 1999). To describe a trade-off between competition and colonization abilities (a CC trade-off), ω is expressed as a continuous decreasing function of c. We retain the classic exponential form (Geritz *et al.* 1999; see Adler & Mosquera 2000):

$$\omega_i \equiv \exp(-\alpha c_i), \tag{1}$$

where α reflects the intensity of the competitive trade-off.

Competition is modelled by a biased competitive lottery. When species i and j compete for a single site, species i obtains the site with probability:

$$\eta_{i,j} \equiv \frac{\omega_i}{\omega_i + \omega_j}. \tag{2}$$

When $\alpha \rightarrow \infty$, the competitive trade-off is infinitely intense, i.e. local competition becomes completely asymmetric as in the original HT model. The value of η for different trade-off intensities is plotted in Fig. 1. The slope of the curve around 0 is $-\alpha/4$ (eqns 1 and 2). Variation in α proportionally translates into variation of this slope, which is

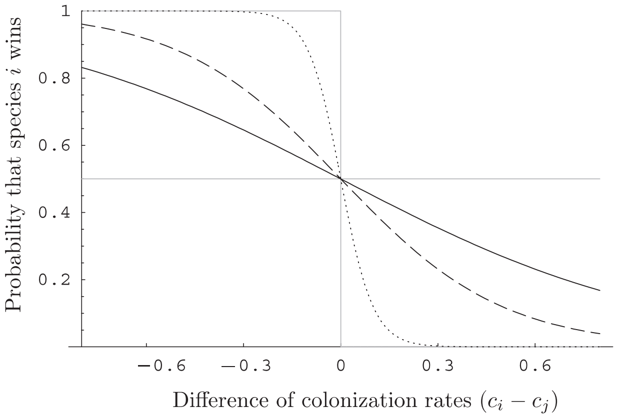

Figure 1 Value of α and local competition asymmetry. The graph plots the value of $\eta_{i,j}$ as a function of the difference between species, $c_i - c_j$. The higher the value of α, the steeper the line. Values of α are 1, 2 and 10. The two limit cases are also plotted (grey lines): the no trade-off case ($\alpha = 0$, horizontal line) and the original Hastings–Tilman model (α infinite, stepwise function).

the criterion stressed by Adler & Mosquera (2000) and also the most amenable to empirical evaluation.

To consider the possibility that colonizing a site already occupied by another species may be intrinsically more difficult than colonizing an empty site, we define γ as the preemption index. γ is the relative probability of settling in an occupied site, i.e. the ratio of the probability of settling in an occupied site over the probability of settling in an empty site. Note that the probability of settling in an empty site is already incorporated in the colonization rate c. When $\gamma = 0$, no displacement (*sensu* Yu & Wilson 2001) is possible and we have a preemption competition model, whereas when $\gamma = 1$ we have the standard dominance competition model (Amarasekare 2003). Note that γ is analogous to May & Nowak's (1994) superinfection rate, yet the situation $\gamma > 1$ will not be considered here, as this would be a form of ecological facilitation.

The resulting model is a system of ordinary differential equations, describing how p_i, the fraction of sites occupied by species i ($i \in [1, n]$), changes with time:

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = c_i p_i \left(1 - \sum_{j=1}^{n} p_j\right) - \mu p_i + \gamma c_i p_i \sum_{j \neq i} p_j \eta_{i,j} - \gamma p_i \sum_{j \neq i} c_j p_j \eta_{j,i} \ \forall i \in [1, n] \tag{3}$$

The first right-hand term describes colonization of empty sites (pure scramble competition) and the second term describes local extinctions (mortality). The last terms correspond to colonization of occupied sites: patches gained after displacing other species (third term) and patches lost after being displaced by other species (fourth term). They incorporate interference competition (*sensu* Adler & Mosquera 2000) between species. When $\alpha \to \infty$ and $\gamma = 1$, this model is exactly the HT model, while when $\gamma = 0$ it is exactly the model of Yu & Wilson (2001). Like the HT model, our model is a competitive Lotka–Volterra model with asymmetric competitive interactions (see Appendix).

Studies of models of coexistence generally consider the maximum number of coexisting species as indicating the power of a model to explain biodiversity. We will rather use the fraction of ecologically stable communities among all possible communities, given some competition modalities. We argue that this fraction is an even more relevant indicator (see Meszéna *et al.* 2006 for a similar argument).

To study the impact of competition parameters (α and γ) on species coexistence, we used analytical as well as Monte Carlo methods to derive the probability that a randomly assembled community is ecologically stable, hereafter called 'probability of coexistence'. By 'randomly assembled' we mean that species are independently drawn from a given regional pool. The probability of coexistence is noted $p_n(\theta)$, where n stands for the number of species in the community and θ is the vector of biological parameters. These parameters are the modalities of competition (α, γ), as well as some features of the environment, namely the perturbation rate (μ) and the maximum colonization rate a species from the regional pool can achieve ($c_{\max}$). Species are clearly limited to some extent in their colonization ability, and as Tilman (1994) found that required colonization rates for coexistence increase very steeply in large communities, $c_{\max}$ is bound to be a drastic constraint on species coexistence.

Analytical investigation is possible for two-species coexistence under some approximations. For more than two species and general parameter combinations, we resort to a Monte Carlo approach (see Kokkoris *et al.* 1999, 2002; Rozdilsky & Stone 2001; Jansen & Kokkoris 2003 for similar approaches). The procedure is as follows. A random community of n species is generated by sequentially drawing species colonization rates from a uniform distribution on the interval $(\mu, c_{\max}]$. We then search for a non-trivial feasible equilibrium of the community (Mathematica notebook available on request). This is performed by evaluating the exact expression of the equilibrium (found by solving $\mathrm{d}p_i/\mathrm{d}t = 0$ for all i, eqn 3) for a given set of parameters θ, and testing if the frequency of every species is strictly positive, and if the sum of frequencies is < 1. Local stability of equilibria is not guaranteed. Thus, every feasible equilibrium was also checked for local stability by computing the eigenvalues of the Jacobian matrix: an equilibrium is locally stable when the real part of every eigenvalue is negative. By repeating this procedure R times for each θ, and recording the number of cases for which such an equilibrium exists, f, we estimate the probability $p_n(\theta)$ as $\hat{p}_n(\theta) = f/R$. R was chosen between 10^4 and 10^6

so as to keep the coefficient of variation of the estimator small enough. This procedure has been applied for two (allowing validation with analytical results), three, four and five species.

RESULTS

Analysis for two species

Niche shadows

A species in a community will prevent some other species from settling in this community. Specifically, under a CC trade-off, a species will prevent an inferior competitor from settling unless the colonization rate of the latter is high enough. The minimum value for this colonization rate reflects a limit to similarity between species (Meszéna *et al.* 2006), and has been referred to as the 'niche shadow' by Kinzig *et al.* (1999). Niche shadows are derived by searching for the conditions that an introduced species must satisfy in order to settle in a resident community.

Consider a single species with strategy c. At equilibrium, it will occupy a fraction p^* of sites, $p^* = 1 - (\mu/c)$ (Levins 1969). A newly introduced species, with strategy c_{I}, will settle in the community if and only if its abundance increases when it is rare. When rare, its abundance p_{I} will change according to the equation:

$$\Delta_{\mathrm{I}} \equiv \frac{1}{p_{\mathrm{I}}}\frac{\mathrm{d}p_{\mathrm{I}}}{\mathrm{d}t} = c_{\mathrm{I}}(1-p^*) - \mu + \gamma c_{\mathrm{I}} p^* \eta_{\mathrm{I}} - \gamma c p^*(1-\eta_{\mathrm{I}}), \tag{4}$$

where η_{I} is the probability that the new species win the competition against the resident species (eqn 2). The introduced species will persist in the community if $\Delta_{\mathrm{I}} > 0$. Solving $\Delta_{\mathrm{I}} > 0$ for c_{I}, and replacing p^* by its value, yields the subset of species that can invade, and the niche shadows (see Fig. 2). When c is large enough, species are so different that their competitive interaction is essentially asymmetric, as when α is infinite. We then approximate the lower boundary for c_{I}, c_{S}, by setting η_{I} to 0 in eqn 4:

$$c_{\mathrm{S}} \approx c + \gamma\frac{c(c-\mu)}{\mu}. \tag{5}$$

With $\gamma = 1$, we recover the invasion criterion for the HT model derived by Tilman (1994). This reflects the well-known limit to similarity between species. In addition, there is a second lower boundary for c_{I}, c_{D}, concerning better competitors (the leftmost niche shadow on Fig. 2). By setting η_{I} to 1, we similarly approximate c_{D}:

$$c_{\mathrm{D}} \approx \frac{c\mu}{\mu(1-\gamma)+\gamma c} \tag{6}$$

This means that there is a limit to dissimilarity in addition to the classical limit to similarity. In other words, some much better competitors will not invade because they are too poor colonizers. Thus, in a CC trade-off model, there are two fundamentally different niche shadows: a limit to similarity, where the worse competitor goes extinct (because of interference competition), and a limit to dissimilarity, where the better competitor goes extinct (because of scramble competition).

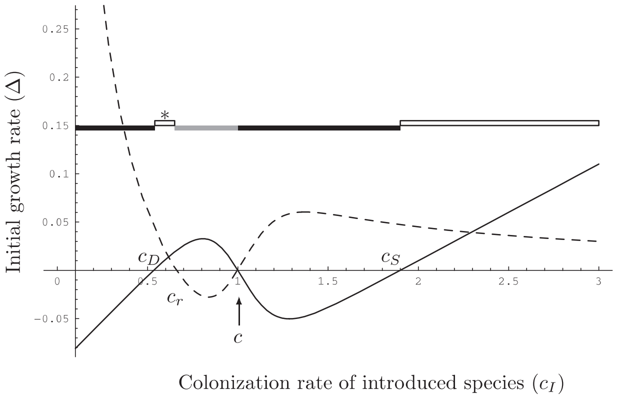

Figure 2 Niche shadows in the two-species case. For a resident species of strategy $c = 1$ (arrow), Δ_{I} is plotted as a function of c_{I} (continuous line). Niche shadows are values for which Δ_{I} is negative (dark bands). Note that there is a niche shadow for c_{I} too different from c (the limit to dissimilarity on the left, noted c_{D}) and for c_{I} too close to c (the limit to similarity, on the right, noted c_{S}). The value of Δ_{I} when the values of c and c_{I} are exchanged is also plotted (dashed line). In the region indicated by a grey band, the introduced species competitively excludes the resident species. Coexistence of the two species is possible only where both functions are positive (white bands). $\Psi(c, \theta)$ is the width of the left white band marked with an asterisk, between c_{D} and c_r. Parameters: $\mu = 0.1$; $\alpha = 100$; $\gamma = 0.1$ for illustrative purposes.

The limit to dissimilarity did not appear in previous models because of the assumption of pure dominance competition ($\gamma = 1$), in which case eqn 6 is the trivial $c_{\mathrm{I}} > \mu$, and only similarity is limited. On the contrary, when $\gamma = 0$ (Yu & Wilson 2001), the limit to similarity vanishes, and only dissimilarity is limited.

In the latter case, as both equations amount to $c_{\mathrm{I}} > c$, any better colonizer can invade and coexistence is impossible (Yu & Wilson 2001). The reason is that the model lacks interference competition (see eqn 3). Interference competition is known to be crucial for coexistence in this model (Adler & Mosquera 2000); otherwise, no force prevents the worse colonizer from being outnumbered by the better colonizer. Coexistence clearly requires that $\gamma > 0$.

With two species in the community, eqn 3 admits at best one non-trivial equilibrium, and no unstable equilibrium can exist (see Appendix). Consequently, an equilibrium exists if and only if the two species can invade each other. Given the strategy of the less competitive species, c_2, we can obtain the range of values of c_1 that would allow coexistence. Let $\Psi(c_2, \theta)$ be the length of this range and c_r its upper limit (see Fig. 2). c_r is obtained by inverting eqn 5 while c_D is given by eqn 6, and we obtain:

$$\Psi(c_2,\theta) = c_r - c_D \approx \frac{\sqrt{\mu(4\gamma c_2 + (1-\gamma)^2\mu)} - (1-\gamma)\mu}{2\gamma} - \frac{c_2\mu}{\gamma c_2 + (1-\gamma)\mu}. \tag{7}$$

If species colonization rates are uniformly distributed within the regional pool, the probability of coexistence of two species is:

$$p_2(\theta) = \frac{2}{(c_{\max} - \mu)^2}\int_{\mu}^{c_{\max}} \Psi(c_2,\theta)\,\mathrm{d}c_2 \tag{8}$$

Replacing $\Psi(c_2, \theta)$ by its approximated value (eqn 7) in eqn 8 yields a close approximation of $p_2(\theta)$. The approximation becomes exact when $c_{\max}\alpha \to \infty$, i.e. for the HT model with any level of preemption. It is expected to be very accurate as long as $c_{\max}$ is not too small.

$c_{\max}$, μ, and requirements for coexistence

Besides $\mu > 0$ and $\gamma > 0$, are there necessary conditions on the other parameters for two species to coexist? As soon as α is finite, there exists a minimum value of $c_{\max}$ below which coexistence is impossible. This value will be called $c_{\min}$. In Appendix S1 (see Supplementary Material), we derive the value of $c_{\min}$. In Fig. 3a, $c_{\min}$ is plotted as a function of α. $c_{\min} \to \infty$ when $\alpha \to 0$. This implies that coexistence is always possible when $\alpha > 0$, i.e. when there is a competitive trade-off, provided $c_{\max}$ is greater than $c_{\min}$.

The value of $c_{\min}$ steadily tends to μ when $\alpha \to \infty$, but it increases very steeply when α becomes very low. $c_{\min}$ tends to be higher when γ is low, but very low values of γ are required for $c_{\min}$ to increase significantly (Fig. 3a). Overall, the necessary conditions for coexistence are:

$$\mu > 0 \quad \text{and} \quad \gamma > 0 \quad \text{and} \quad \alpha > 0 \quad \text{and} \quad c_{\max} > c_{\min}. \tag{9}$$

When $c_{\max}$ is too close to $c_{\min}$, it is a severe constraint on coexistence as soon as α is finite or $\gamma < 1$. Except for the HT model, increasing $c_{\max}$ thus initially increases the probability of coexistence (Fig. 3b). Yet a threshold value is quickly attained, beyond which the probability of coexistence diminishes steadily to 0 as $c_{\max}$ tends to infinity (Fig 3b). The threshold value for $c_{\max}$ is generally low and corresponds to communities in which species are strongly limited by colonization.

In the following, we present results for $\mu = 0.1$, the value most commonly used in Tilman (1994).

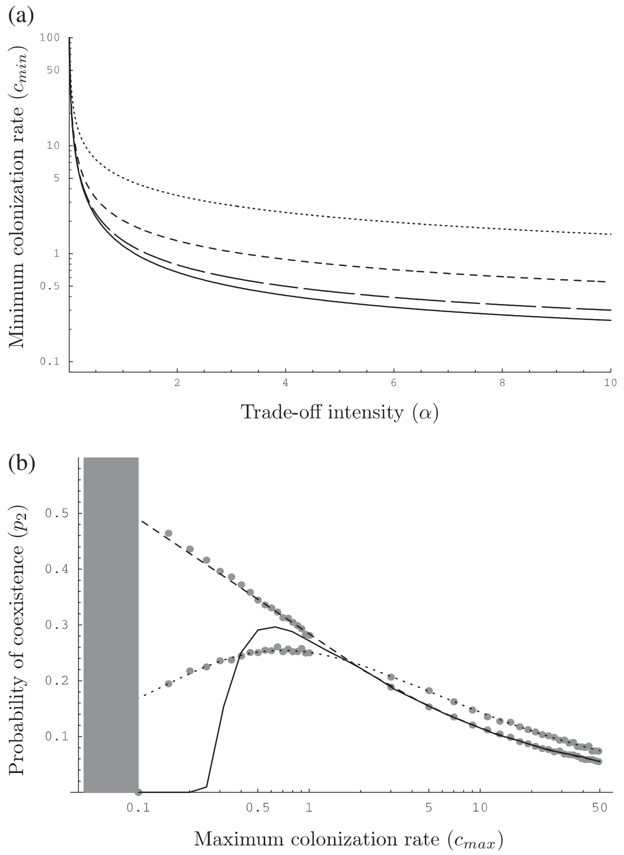

Figure 3 (a) Minimum colonization rate for coexistence ($c_{\min}$, log scale) as a function of trade-off intensity (α). Continuous line: $\gamma = 1$, long dashed line: $\gamma = 0.5$, short dashed line: $\gamma = 0.1$, dotted line: $\gamma = 0.01$. Parameters: $\mu = 0.1$. (b) Probability of coexistence of two species $p_2(\theta)$ as a function of $c_{\max}$ (log scale). Species are not viable in the shaded region because $c < \mu$. Dashed line: exact values for α infinite and $\gamma = 1$ (Hastings–Tilman model), dotted line: exact values for α infinite and $\gamma = 0.5$. Corresponding Monte Carlo estimations are figured by grey points. Continuous line: Monte Carlo estimations for $\gamma = 1$ and $\alpha = 10$. In this case coexistence requires $c_{\max}$ to exceed a threshold value ($c_{\min}$). Note the perfect fit between Monte Carlo and analytical results when α is infinite, and the close agreement when $\alpha = 10$ and $c_{\max}$ is not too small. Parameters: $\mu = 0.1$.

Probabilities of coexistence: general case

Stability of equilibria

All feasible equilibria we found were locally stable, strongly suggesting that any feasible equilibrium is locally stable. This is not unexpected, as this property holds for the HT model (Tilman 1994), which is a limit case of our model (see Appendix). We also numerically iterated eqn 3 for three, four and five species, with different sets of parameters and initial conditions. In all cases, the dynamics converged to the predicted equilibrium. This suggests that most equilibria are not only locally, but also globally, stable.

Effect of competition asymmetry

Decreasing trade-off intensity (α) is expected to make coexistence more difficult or impossible (Adler & Mosquera 2000; Levine & Rees 2002). This is indeed what we find (Fig. 4). Yet the probabilities of coexistence increase steeply to a plateau where they are very close to the value for infinite α. This means that weakening the intensity of the trade-off does not affect the probability of coexistence much, unless α becomes quite low, in which case local competition becomes too symmetric, $c_{\min}$ gets close to $c_{\max}$ and the probability of coexistence collapses.

Necessarily, increasing the number of species decreases the probability of coexistence. All else being equal, we could expect the probability of coexistence to decrease geometrically with the number of species, owing to the increasing dimensionality of the system. This is grossly what happens for infinite α (Fig. 4). Apart from this, the larger the number of species, the higher the value of α below which the probability of coexistence drops (Fig. 4). But coexistence remains possible, even if improbable, for very low values of α. We can estimate an upper boundary for the minimum value of α allowing coexistence: it seems to increase with the number species, but remains low even for five species (see Fig. 4).

When $c_{\max}$ increases, coexistence is possible for lower values of α. One reason is that, as $c_{\max}$ increases, the mean difference between species in the community becomes larger, and as a result the mean interaction between species can become quite asymmetric despite the competitive trade-off itself being far from stepwise (see Fig. 1). Thus, the value of α is best discussed in relation to the value of $c_{\max}$. For all parameter values discussed in this paper, we checked the distribution of interaction strength between species among stable equilibria (data not shown): non-stepwise interactions are frequent, showing that stepwise interactions are not crucial to coexistence.

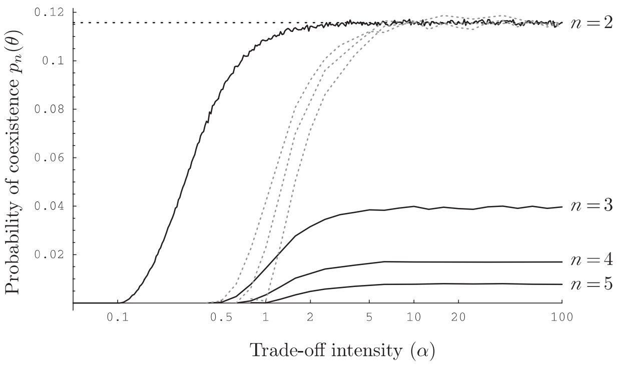

Figure 4 Trade-off intensity (α) and probabilities of coexistence. Probabilities of coexistence for n species (n = 2, 3, 4 and 5 species), as a function of α (log scale). For two species, the analytically derived (asymptotic) value for α infinite is also plotted (horizontal dotted line). Dotted lines are the curves for three, four and five species, scaled on the asymptotic value for two species. This helps visualize the relative effect of trade-off intensity. Parameters: $\gamma = 1$; $\mu = 0.1$; $c_{\max}=10$.

Effect of preemption

γ strongly affects coexistence, even with a stepwise competitive trade-off (α infinite, Fig. 5). As noted above, coexistence is impossible under pure preemption competition ($\gamma = 0$, Yu & Wilson 2001), whereas it is fairly easy under dominance competition ($\gamma = 1$, Tilman 1994). One could expect the probabilities of coexistence to increase more or less steadily with increasing γ. This is not the case, and preemption can have contrasting effects on coexistence, depending on $c_{\max}$. A saturating relation is obtained in some cases, such that introducing preemption modestly affects coexistence unless competition becomes truly preemptive (i.e. $\gamma < 0.5$). But in many cases, the relation is not monotonic: there is an intermediate optimum of γ maximizing the probability of coexistence, indicating that some preemption can favour coexistence. The optimal value of γ decreases with increasing $c_{\max}$ (Fig. 5).

The effect of γ in relation to $c_{\max}$ is analysed further in Appendix S2. For two species and fully asymmetric local competition, preemption will disfavour coexistence only if $c_{\max}$ is less than roughly 13 times the perturbation rate (see Fig. 5a). This means that the best possible colonizer would occupy *c.* < 90% of the available patches at equilibrium, if it was freed of all its competitors. In such communities, which are strongly limited by colonization, preemption disfavours coexistence, while in all other communities, some degree of preemption is favourable to coexistence. The optimal level of preemption can be very low, especially when $c_{\max}$ is large. Actually it tends to 0 when $c_{\max} \rightarrow \infty$ (Appendix S2).

This effect of γ is even stronger when local competition is not fully asymmetric (Fig. 6). When the intensity of the trade-off (α) is decreased, the relative increase of the probability of coexistence with preemption is larger, and the optimum value of γ becomes even lower (Fig. 6). The effect can be strong, especially with several species (Fig. 6b). Of course, decreasing α further eventually makes the community limited by colonization because $c_{\min}$ comes close to $c_{\max}$. In this case, the optimum value of γ first rises again (Fig. 6), and eventually dominance competition ($\gamma = 1$) becomes optimal (Fig. 6a).

The positive effect of preemption can be explained by consideration of niche shadows in the two-species case: decreasing γ simultaneously decreases the width of the limit to similarity (eqn 5) and increases the limit to dissimilarity (eqn 6). A change in γ acts in two opposite directions on

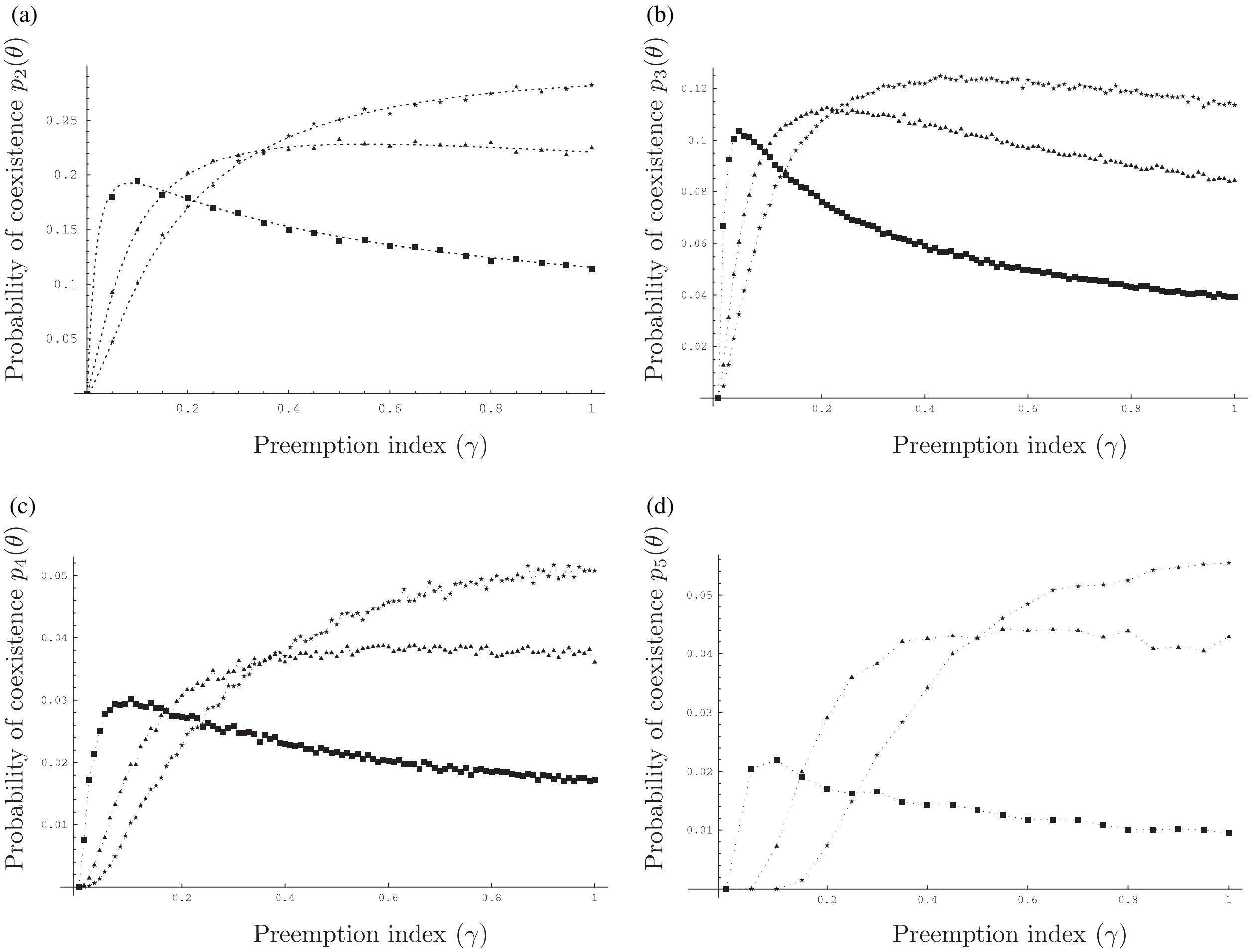

Figure 5 Effect of preemption (γ) on the probability of coexistence when the competitive trade-off is infinitely intense (α infinite). Probability of coexistence of (a) two, (b) three, (c) four and (d) five species. $c_{\max} = 1$ (stars), 2 (triangles) and 10 (boxes). Dotted lines for two species represent the exact analytical values. Parameters: $\mu = 0.1$; α infinite.

niche shadows, and does not have a simple effect on coexistence: if the marginal increase of the limit to dissimilarity exceeds the marginal decrease of the limit to similarity, then overall it will reduce coexistence, while if the reverse is true, overall it will increase coexistence. We also see that the limit to similarity increases linearly with γ, while the limit to dissimilarity decreases as γ^{-1}: an initial increase of γ from 0 should mostly decrease the limit to dissimilarity, promoting coexistence, while a further increase should essentially enlarge the limit to similarity, restraining coexistence. This helps understand the non-monotonic effect of γ on coexistence. The interplay between the niche shadows is illustrated graphically in Appendix S2.

DISCUSSION

The CC trade-off model has been severely criticized over the past 10 years. Several authors have suggested that this trade-off cannot account for the coexistence of species when not coupled to an additional force of coexistence (Amarasekare 2003). We showed here that two of the main critiques are probably overstated. Starting from the original model (Hastings 1980; Tilman 1994), we relaxed the assumptions of a stepwise competitive trade-off and of pure dominance competition, and coexistence is far from being precluded.

As expected, relaxing the intensity of the competitive trade-off reduces the scope for coexistence (Geritz *et al.* 1999; Levine & Rees 2002; Amarasekare 2003). But coexistence is always possible provided colonization rates are high enough ($c_{\max} > c_{\min}$). As a result, decreasing trade-off intensity can be balanced by increasing $c_{\max}$, and probabilities of coexistence are little affected unless local competition truly approaches symmetry. Accordingly, this result might be sensitive to the precise shape of the trade-off between ω and c (Adler & Mosquera 2000; but see

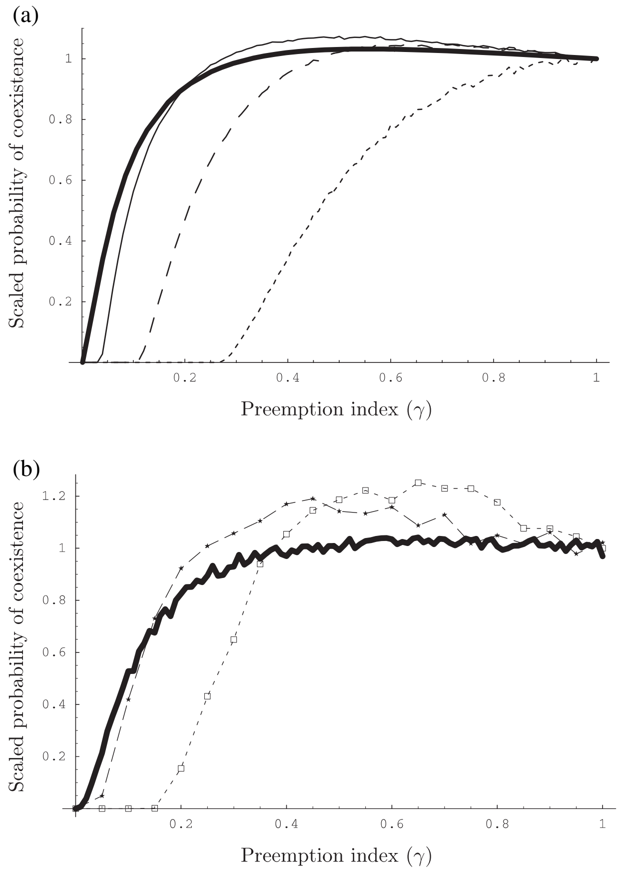

Figure 6 Effect of preemption (γ) for various values of α. (a) Probability of coexistence of two species. For each α, probabilities are scaled to be 1 when $\gamma = 1$ (pure dominance competition). The absolute probabilities of course depend on α, as shown in Fig. 4. α infinite (thick continuous line), $\alpha = 2$ (thin continuous line), $\alpha = 1$ (dashed line) and $\alpha = 0.7$ (dotted line). (b) Probability of coexistence of four species. For each α, probabilities are scaled to be 1 when $\gamma = 1$. α infinite (thick continuous line), $\alpha = 5$ (dashed line with stars) and $\alpha = 3$ (dotted line with boxes). Parameters: $c_{\max}=2$; $\mu = 0.1$.

Banks 1997), even if we retained a trade-off function that is commonly used, and which has been used in previous studies addressing coexistence by a CC trade-off (e.g. Geritz *et al.* 1999). In fact this result should hold provided that the trade-off function $\eta_{i,j}$ tends to 1 when $c_i - c_j \to -\infty$ and tends to 0 when $c_i - c_j \to \infty$. The crucial point is then to know whether very low trade-off intensities are frequent in nature, and to what extent colonization rates can be high enough to allow coexistence in this case. Trade-off parameters are notoriously hard to estimate from empirical data, making it difficult to figure out what values of α are likely to be found in natural communities. For annual plant communities, an experiment from Goldberg & Landa (1991) indicates low trade-off intensities. Although a good estimation of α is difficult, fitting the slope of $\eta_{i,j}$ in our model to the slope of competition coefficients estimated from the data set (the value of s in Levine & Rees 2002) yields to α somewhere around 1 or 2. Independent data for plants suggest high values of $c_{\max}$, which could compensate for the weak competitive trade-off. More data are badly required, but our results at least suggest that stepwise (hierarchical) competition is not as critical a factor as is sometimes argued.

Incidentally, the existence of $c_{\min}$ rules out infinite niche packing (Kinzig *et al.* 1999) in the model when α is not infinite (Adler & Mosquera 2000). We also predict coexistence of more species than one would from Fig. 5a of Adler & Mosquera (2000). This is probably because we are interested in ecologically stable communities and not invasion-resistant communities: invasion-resistant communities seem to harbour much fewer species than could coexist for a given intensity of the trade-off.

Relaxing the assumption of pure dominance competition (i.e. introducing preemption) leads to fairly surprising results. As no coexistence is possible under pure preemption competition (Yu & Wilson 2001), whereas it is rather easy under dominance competition (Tilman 1994), preemption is considered detrimental to coexistence. This even led some authors to declare the death of the CC trade-off model (Yu & Wilson 2001). We show that one cannot interpolate in this way from the two extreme cases: introducing some preemption is not detrimental to coexistence, and over a large set of conditions, it even favours coexistence. Introducing preemption has a major qualitative effect by creating a limit to dissimilarity. In a general CC trade-off model, niche shadows are thus of two types: the classical limit to similarity (failure of the worst competitor) and the limit to dissimilarity (failure of the best competitor). Preemption decreases the limit to similarity, but increases the limit to dissimilarity. Its overall effect depends on the interplay of these two niche shadows. As a consequence, there is an optimal level of preemption that maximizes coexistence, and this level is often quite high.

If γ is interpreted more broadly (see Nowak & May 1994), it may take values beyond 1 and can be seen as a factor governing the ratio between scramble and interference interspecific competition (Amarasekare 2002). Our results suggest overall that there is an optimal scramble/interference ratio for coexistence. Note that the limit to dissimilarity probably rules out coexistence of an infinite number of species.

The positive effect of preemption proves to be stronger when the competitive trade-off is not very intense, as long as the community remains not strongly limited by colonization. Thus, moderate trade-off intensities, which might be more frequent in nature (Banks 1997; Levine &

Rees 2002), make preemption even more favourable to coexistence.

Competition has been considered here in the light of some environmental constraints, $c_{\max}$ and μ. Although $c_{\max}$ plays an important role, previous studies essentially considered no upper bound to colonization rates (Tilman 1994). We showed, for instance, that if communities are strongly limited by colonization (e.g. dispersal or fecundity), dominance competition is more favourable to coexistence, whereas if species can disperse more, this is no longer the case, and some preemption favours coexistence. $c_{\max}$ acts like a bifurcation parameter for the effect of preemption in this model. It also plays a major role because as long as it is greater than $c_{\min}$, coexistence is possible even for very low trade-off intensities. $c_{\max}$ could vary across environments because of the identity of the main vectors of dispersion, climatic conditions or human activity, and it can be seen as a surrogate for productivity (Kondoh 2001).

The spatially implicit modelling framework used here, although unrealistic, has been shown to be unfavourable to species coexistence (Hurtt & Pacala 1995; Higgins & Cain 2002). Incorporating spatially limited dispersal into our model is then likely to further promote coexistence. The same conclusion holds for the assumption of instant local dynamics (Higgins & Cain 2002). Another potentially unrealistic feature of our model is that the preemptive advantage is acquired immediately after colonization. Despite instantaneous local demography, preemption could slowly increase after colonization, possibly on the regional time scale. This would amount to increasing γ for newly colonized patches. Consequently, γ would increase mostly for poor competitors because their turnover is higher and their local populations are on average younger. The overall effect would amount to increasing the limits to similarity and to decreasing the limits to dissimilarity, just as a global increase of γ would do in our model.

Another limitation to coexistence, which we did not address in the present work, is demographic stochasticity with a finite number of sites (Goldwasser *et al.* 1994). With an individual (safe-site) interpretation of the model, the number of sites can be quite large. Nevertheless, because of demographic stochasticity, it is probably utopic to consider the long-term coexistence of more than *c.* 10 species in this model. Note that this is no way specific: demographic stochasticity hinders coexistence in any model (Tilman 2004). The CC trade-off model deals with closely allied species, sharing the same resources in a homogeneous landscape and within a single trophic level. In this sense it is a simplified model, and the coexistence of a guild of as few as five species is not negligible: many such guilds could coexist in a complete community, one for every resource for instance, and several in each trophic level. The biodiversity considered here can indeed be embedded within other mechanisms of coexistence, such as niche partitioning or food-web construction (Amarasekare *et al.* 2004).

Spatial competitive trade-offs play a major role in community ecology, and also have important applications for epidemiology. We have shown that the CC trade-off model is not yet dead, and have highlighted the important and intricate roles of preemption and colonization limitation. 'Fully preemptive' or 'mostly preemptive' can indeed make a great deal of difference. And 'mostly preemptive' might well be the rule, because stochasticity is likely to make full preemption difficult to achieve in real-life situations. Estimating trade-off intensities in the field remains an important objective for these models (Banks 1997), but empirical efforts should also be devoted to document preemption and colonization limitation.

APPENDIX

1. With two species, isoclines are two lines in the plane (p_1, p_2), intersecting at the equilibrium point (p_1^*, p_2^*). Each isocline intersects the p_1-axis at values $O_{1,1}$ and $O_{1,2}$, and the p_2-axis at values $O_{2,1}$ and $O_{2,2}$.

From eqn 3:

$$\begin{cases} O_{1,1} = 1 - \mu/c_1 \\ O_{2,2} = 1 - \mu/c_2 \\ O_{1,2} = \frac{c_2-\mu}{c_2-\gamma(\eta_{1,2}c_1-\eta_{2,1}c_2)} \\ O_{2,1} = \frac{c_1-\mu}{c_1-\gamma(\eta_{1,2}c_1-\eta_{2,1}c_2)} \end{cases}$$

An unstable equilibrium would occur in the case $O_{1,1} > O_{1,2}$ and $O_{2,2} > O_{2,1}$. With $c_2 > c_1$ and thus $\eta_{1,2} > 0.5$, these conditions cannot be met, and no unstable equilibrium can exist, independently of the shape of the trade-off function.

2. We can rewrite eqn 3 to match the general Lotka–Volterra formulation:

$$\frac{dp_i}{dt} = p_i(c_i - \mu)\left[1 + \sum_{j=1}^{n} p_j \frac{\gamma(c_i\eta_{i,j} - c_j\eta_{j,i}) - c_i}{c_i - \mu}\right].$$

Here $c_i - \mu$ is the intrinsic growth rate of species *i*, and the fraction on the right-hand side is the Lotka–Volterra interaction coefficient $\alpha_{i,j}$. As $\alpha_{i,j} < 0 \; \forall \; i,j$, this is a competitive Lotka–Volterra model. Moreover, most of the time $\alpha_{i,j} \gg \alpha_{j,i}$, which means that competition is asymmetric (Kokkoris *et al.* 2002).

3. All parameter values considered in the present study amount to decreasing α and/or γ relative to the HT model. Decreasing γ decreases both the mean and variance of interaction coefficients, while decreasing α reduces only their variance. In both cases, the hierarchical structure of the interaction matrix is preserved. Given the results of Kokkoris *et al.* (2002) and Jansen & Kokkoris (2003), we

indeed expect all equilibria of our model to be stable too. This property seems common in competitive Lotka–Volterra systems (Rozdilsky & Stone 2001).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from http://www.Blackwell-Synergy.com:

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

Appendix S2 Optimal level of premption 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 μ_i, obeys the differential equation

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = \left[c_i\left(1 - \sum_{j\in S} p_j\right) - \mu_i + \gamma c_i \sum_{j\in S} \eta_{i,j} p_j - \gamma \sum_{j\in S} c_j \eta_{j,i} p_j\right] p_i. \tag{1}$$

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 γ describes the strength of the pre-emptive effect. The pool of available species is given by the set 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 γ, which can be < 1.
5. Stochastic assembly: the set 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.