

Appendix A: Model details

Spatially implicit model

We initially assume that c and e are fixed for both species in both patches and model changes in the proportions of each patch-type-occupancy in the metacommunity where p_{ij} denotes the proportion of patches of type j occupied by species i . We note that the dynamics of empty patches of each type are completely dependent on the dynamic of occupied patches and can be calculated from them by subtraction. The equations of the model are:

$$\frac{dp_{1a}}{dt} = c(p_{1a} + p_{1b})(h_a - p_{1a}) - ep_{1a} \quad (A.1)$$

$$\frac{dp_{2a}}{dt} = c(p_{2a} + p_{2b})(h_a - p_{1a} - p_{2a}) - cp_{2a}(p_{1a} + p_{1b}) - ep_{2a} \quad (A.2)$$

$$\frac{dp_{1b}}{dt} = c(p_{1a} + p_{1b})(h_b - p_{1b} - p_{2b}) - cp_{1b}(p_{2a} + p_{2b}) - ep_{1b} \quad (A.3)$$

$$\frac{dp_{2b}}{dt} = c(p_{2a} + p_{2b})(h_b - p_{2b}) - ep_{2b} \quad (A.4)$$

In the absence of extinctions (the species sorting case), the model would predict that at equilibrium, all a patches are occupied by species 1 and all b patches by species 2 (i.e, $p_{1a}=h_a, p_{2b}=h_b$). We are interested in how this changes as c and e differ from zero.

We analyze the system by considering possible equilibria, their feasibility, and their stability. When letting equations A.1-A.4 be zero, six equilibrium solutions may be found:

The first equilibrium is :

$$\begin{aligned} p_{1a}^* &= 0 \\ p_{1b}^* &= 0 \\ p_{2a}^* &= 0 \\ p_{2b}^* &= 0 \end{aligned} \quad (A.5)$$

This equilibrium position corresponds to the extinction of all species in the metacommunity.

The second equilibrium is:

$$\begin{aligned} p_{1a}^* &= h_a \left(1 - \frac{e}{c}\right) \\ p_{1b}^* &= h_b \left(1 - \frac{e}{c}\right) \\ p_{2a}^* &= 0 \\ p_{2b}^* &= 0 \end{aligned} \quad (A.6)$$

The third equilibrium is:

$$\begin{aligned} p_{1a}^* &= 0 \\ p_{1b}^* &= 0 \\ p_{2a}^* &= h_a \left(1 - \frac{e}{c}\right) \\ p_{2b}^* &= h_b \left(1 - \frac{e}{c}\right) \end{aligned} \quad (A.7)$$

Which is the equilibrium where only species 1 remains.

Which is the symmetrical equilibrium, for species 2.

The fourth equilibrium is:

$$\begin{aligned}
 p_{1a}^* &= \frac{ch_a - eh_b}{e + c} \\
 p_{2a}^* &= \frac{e(ch_b - eh_a)}{c(e + c)} \\
 p_{1b}^* &= \frac{e(ch_a - eh_b)}{c(e + c)} \\
 p_{2b}^* &= \frac{ch_b - eh_a}{e + c}
 \end{aligned} \tag{A.8}$$

Which is an equilibrium where the two species coexist in the metacommunity (they do not coexist locally in any patch however).

The fifth equilibrium is:

$$\begin{aligned}
 p_{1a}^* &= \frac{-2e + c(2h_a + 1) - \sqrt{4e^2 + c^2(1 - 4h_a h_b) - 4ce}}{4c} \\
 p_{2a}^* &= \frac{2e - c(2h_a + 1) + \sqrt{4e^2 + c^2(1 - 4h_a h_b) - 4ce}}{4c} \\
 p_{1b}^* &= \frac{2e - c(2h_b + 1) - \sqrt{4e^2 + c^2(1 - 4h_a h_b) - 4ce}}{4c} \\
 p_{2b}^* &= \frac{-2e + c(2h_b + 1) + \sqrt{4e^2 + c^2(1 - 4h_a h_b) - 4ce}}{4c}
 \end{aligned} \tag{A.9}$$

which is a second equilibrium where coexistence may happen.

The final possible equilibrium is:

$$\begin{aligned}
p_{1a}^* &= \frac{-2e + c(2h_a + 1) + \sqrt{4e^2 + c^2(1 - 4h_a h_b) - 4ce}}{4c} \\
p_{2a}^* &= \frac{2e - c(2h_a + 1) - \sqrt{4e^2 + c^2(1 - 4h_a h_b) - 4ce}}{4c} \\
p_{1b}^* &= \frac{2e - c(2h_b + 1) + \sqrt{4e^2 + c^2(1 - 4h_a h_b) - 4ce}}{4c} \\
p_{2b}^* &= \frac{-2e + c(2h_b + 1) - \sqrt{4e^2 + c^2(1 - 4h_a h_b) - 4ce}}{4c}
\end{aligned} \tag{A.10}$$

There are strict boundaries of existence for these equilibria. For one thing it is not possible for any p to go below 0. For another thing, p_{ij} cannot go above h_j .

The equilibrium without species (equation A.5) is of course always possible.

For equilibria with one species (equations A.6 or A.7), the necessary condition is:

$$c > e \tag{A.11}$$

For the fourth equilibrium (equation A.8) to exist, it is necessary that

$$c > e \max\left(\frac{h_b}{h_a}, \frac{h_a}{h_b}\right) \tag{A.12}$$

The two last equilibria (equations A.9 and A.10) are not possible. Indeed, for each of these, note that if p_{1a}^* is positive, then p_{2a}^* is necessarily negative, the same being true for frequencies in patch of b type.

Since four equilibria are possible in this system, it is necessary to know which one of them is the outcome of the dynamics and under what conditions. To determine the stability of the equilibrium it is necessary to compute the Jacobian matrix of the system.

J

$$= \begin{bmatrix} -e + c(h_a - 2p_{1a}^* - p_{1b}^*) & 0 & c(h_a - p_{1a}^*) & 0 \\ c(h_b - p_{1b}^* - p_{2b}^*) & -c p_{1b}^* & -e + c(h_b - 2p_{1b}^* - p_{1a}^* - 2p_{2b}^* - p_{2a}^*) & -c(p_{1a}^* + 2p_{1b}^*) \\ -c(p_{2b}^* + 2p_{2a}^*) & -e + c(h_a - 2p_{1a}^* - p_{1b}^* - 2p_{2a}^* - p_{2b}^*) & -c p_{2a}^* & c(h_a - p_{1a}^* - p_{2a}^*) \\ 0 & c(h_b - p_{2b}^*) & 0 & -e + c(h_b - 2p_{2b}^* - p_{2a}^*) \end{bmatrix} \quad (A.13)$$

Using this Jacobian matrix it is possible to show that if existence condition is fulfilled for the coexistence equilibrium (equation A.8), then this equilibrium is also stable. Our study thus requires this condition.

The proof of this goes as follow. Given the coexistence equilibrium shown in (A.8), the equilibrium is locally stable if and only if the eigenvalues of the related Jacobian matrix (A.13) all have negative real parts. Such eigenvalues can be computed, and, considering the values of occupancy at equilibrium (equations A.8), simplified into:

$$\begin{aligned} \lambda_1 &= e - c \\ \lambda_2 &= -c \\ \lambda_3 &= \frac{-1}{2(e+c)} \left(e^2 + c^2 + (ce + c^2) \sqrt{\frac{(h_a - h_b)^2 (c^4 + 4c^3e + 4ec^3 + e^4) + 2c^2e^2 (5h_a^2 - 2h_a h_b + 5h_b^2)}{c^2 (c+e)^2}} \right) \\ \lambda_4 &= \frac{-1}{2(e+c)} \left(e^2 + c^2 - (ce + c^2) \sqrt{\frac{(h_a - h_b)^2 (c^4 + 4c^3e + 4ec^3 + e^4) + 2c^2e^2 (5h_a^2 - 2h_a h_b + 5h_b^2)}{c^2 (c+e)^2}} \right) \end{aligned} \quad (A14)$$

Given that the coexistence equilibrium requires that $c > e$ (equation (A.12) being a stronger condition than equation (A.11)), it is straightforward that λ_1 is real and negative.

Similarly, λ_2 is both real and negative. While λ_3 is more complex, note that the term below the square root is always positive, so that λ_3 is real in all cases. λ_3 is also negative, as all terms that compose it are positive, except for the -1 at the numerator.

The most complex eigenvalue to study is λ_4 . Let us first note that, were we to consider this eigenvalue λ_4 as a function of c , four roots would exist for the function, *i.e.*, four

values of c makes λ_4 null. Assuming, without loss of generality that A patches dominate ($h_a > h_b$), one of these roots is the boundary of coexistence $c = e^{\frac{h_a}{h_b}}$. Although the three other roots are formally complex, it is possible to show that they are all inferior to $e^{\frac{h_a}{h_b}}$. Therefore, between $e^{\frac{h_a}{h_b}}$ and larger values of c (i.e. the ones that allow the coexistence), the eigenvalue λ_4 does not change sign. Now consider the limit of λ_4 for large values of c , note that:

$$\lim_{c \rightarrow +\infty} \lambda_4 = c^2 \left(-1 + \sqrt{(h_a - h_b)^2} \right) \quad (A.15)$$

Noting that this value is necessarily negative, we conclude that the eigenvalue λ_4 , which is always real, is null at the boundary condition of species coexistence, but negative for all values above (i.e. for all values effectively allowing coexistence).

Therefore, when the two species coexist, all eigenvalues are real and negative, so that the coexistence is always locally stable.

Our model so far is highly simplified and we can consider numerous possible complications. One is that extinctions may not be independent of species occupancies since species may be less likely to go extinct in patches where they are dominant than where they are subordinate regardless of competition between them. We model this by giving each species an advantage in its preferred patch by reducing its extinction rate, multiplying it by a factor $k \in [0, 1]$.

The analytical solution to this model is more difficult than for (A.1-4) so we provide simulations instead. When the advantage is not too strong (e.g., $k = 0.5$), the results are roughly similar to the case where there is no advantage. However when the advantage is strong enough (e.g., $k = 0.1$) the critical threshold conditions for alternate one-species

equilibria disappear. There is still however a strong relationship between extinction rate and the prevalence of empty patches and the occupancy of patches by subordinate species.

The spatially explicit model: patch dynamics on a lattice

Simulations were carried on a grid of 30x30 patches. Patches could be of type a or of type b , with probabilities h_a and h_b respectively. We start with the first patch type and attribute a patch type at random to each cell. We study the dynamics on such random lattices (figure 3A-B). We also study the dynamics on non-random lattices (figure 3C-D). To produce such lattices, we use the “force to be full” algorithm described in Mangel et al. (1994). The use of “force to be full” requires two additional parameters: p_l , the probability that a patch is of the same type a , knowing that the neighbor patch is of type a , and a parameter β that describes the scale on which a given locality type affects the probability for another locality to be on the same type. Here we take $p_l=0.85$ and $\beta=0.25$. Associating these two parameters, a function can be defined that describe, given the state of one patch, the probability that another "destination patch" at a distance d will be of the same type. Because this "destination patch" also undergoes the influence of other patches on the grid, its final state is determined by summing the "forces" (ie, the associated probability functions) coming from all other patches. These "forces" are weighted depending of distance from source patches as $\exp(-\beta*d)$, so that the parameter β scales the influence of patches depending on their distance. Full details of the method and of how it can be implemented in 2 or 3 dimensional cases can be found in Mangel et al. (1994). Changes in β or p_l do not affect the qualitative patterns shown on Fig. 4.

Each time step is divided in two events: colonization and extinction. During the colonization phase, a patch is colonized by a species of type i with probability $c * n_i / 8$ where n_i is the total number of patches occupied by species i in the eight neighbor patches. Consistent with the hypothesis from the non-explicit model, colonization leads to replacement only if the target patch is empty or if the colonizer is dominant over the resident. During the extinction process, a population has a probability e of going extinct. Simulations are started with one third of the patch occupied by each of the two species types, one third of the landscape being empty. Simulations are run for 1000 time steps. This amount of time is largely superior to the time (100) needed for the proportion of patches occupied by each species type to stabilize. Additional simulations (not shown) indicate that our results are robust to such initial conditions.

On the final community, we perform a partitioning of the observed variation among spatial and environmental components following the general method of Cottenie (2005) except that we implemented eigenvector maps to study spatial effects instead of polynomial fitting (see Peres-Neto et al. 2006). Eigenvector maps using the PCNM (Principle Components on Neighborhood Matrices) is a sophisticated method of spatial analysis that allows spatial patterns at different spatial scales to be quantified. Although the dynamical process described above is carried out on a 30*30 grid, the analysis is made on the inner central 20*20 subset grid, to avoid edge effects. Analysis of such edge effects showed that they do not influence our results: patterns shown on Figure 3 were quantitatively similar whether the edge was excluded (as we did) or not. Results are shown on Figure 3 for a random and for a highly correlated landscape. We checked the robustness of our results for various combinations of colonization (c), landscape evenness

(ratio h_a/h_b), dispersal procedure (dispersal from the 8 neighbor patches, the 24 neighbor patches, or from the whole landscape) and spatial autocorrelation and found them to be remarkably robust both qualitatively and quantitatively.

LITERATURE CITED

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