

Supplementary Material 1

A metapopulation model with the total number of patches

Here we extend the Levins metapopulation framework to incorporate explicitly the total number of patches. Let N be the number of patches occupied by local populations.

Then the rate at which the number of occupied patches increases is expressed as

$$mN\left(\frac{T-N}{T}\right)s, \quad (\text{S1})$$

where T is the total number of patches; m is the realized number of propagules originating from a local parental population per unit time (see below). A propagule is defined here as a group of individuals originating from a local parental population and colonizing a new patch. $(T-N)/T$ is the probability that a patch reached by a propagule is vacant; and s is the probability that a propagule in a vacant patch successfully establishes a local population. We consider that a local parental population produces a certain number, M , of propagules per unit time. When the total number of patches is large enough to exceed this number (i.e., $T > M$), all propagules will have patches to go (while the target patch may or may not be occupied by the same species); thus, the realized number of propagules corresponds to M (i.e., $m = M$).

When the total number of patches is smaller than the number of propagules produced (i.e., $T \leq M$), some propagules fail to find target patches and the realized number of propagules is limited by the total number of patches (i.e., $m = T$). Formally,

$$m = \begin{cases} T & (T \leq M) \\ M & (T > M) \end{cases}. \quad (\text{S2})$$

Further, as in the classic metapopulation framework, we assume that the rate at which a local population goes extinct is e . These assumptions yield a differential equation that

describes the dynamics of the number of local populations:

$$\frac{dN}{dt} = mN \left(\frac{T-N}{T} \right) s - eN. \quad (\text{S3})$$

Denoting the frequency of patches occupied by local populations as $p = N/T$, the equation becomes

$$\frac{dp}{dt} = smp(1-p) - ep. \quad (\text{S4})$$

To be more explicit about the functional forms depending on T , the model is written as

$$\frac{dp}{dt} = \begin{cases} sTp(1-p) - ep & (T \leq M) \\ sMp(1-p) - ep & (T > M) \end{cases}. \quad (\text{S5})$$

We may solve for the equilibrium frequency of occupied patches by setting the right hand side equal to zero:

$$\bar{p} = \begin{cases} 0 & \left(0 \leq T \leq \frac{e}{s} \right) \\ 1 - \frac{e}{sT} & \left(\frac{e}{s} < T \leq M \right) \\ 1 - \frac{e}{sM} & (T > M) \end{cases}. \quad (\text{S6})$$

There is a necessary condition for a feasible internal equilibrium to exist: $e/s < M$.

The full model

The full model for the frequency dynamics of patches of different states is

$$\begin{aligned} \frac{dp_B}{dt} &= s_{1A}m_1(p_B + p_C + p_D + p_E)p_A + e_{1C}p_C + e_{1D}p_D \\ &- s_{2B}m_2(p_C + p_E)p_B - s_{3B}m_3(p_D + p_E)p_B - e_{1B}p_B, \end{aligned} \quad (\text{S7a})$$

$$\frac{dp_C}{dt} = s_{2B}m_2(p_C + p_E)p_B + e_{3E}p_E - s_{3C}m_3(p_D + p_E)p_C - (e_{1C} + e_{2C})p_C, \quad (\text{S7b})$$

$$\frac{dp_D}{dt} = s_{3B}m_3(p_D + p_E)p_B + e_{2E}p_E - s_{2D}m_2(p_C + p_E)p_D - (e_{1D} + e_{3D})p_D + ap_E, \quad (\text{S7c})$$

$$\frac{dp_E}{dt} = s_{2D}m_2(p_C + p_E)p_D + s_{3C}m_3(p_D + p_E)p_C - (e_{1E} + e_{2E} + e_{3E})p_E - ap_E, \quad (\text{S7d})$$

where s_{iX} is the probability that a propagule population of species i establishes a local population in a patch of state X ; and e_{iX} is the extinction rate of a local population of species i in a patch of state X due to local disturbance; and other symbols are explained in the main text. The simpler model in the main text is derived by assuming that the probabilities that propagules of species i establish a local population do not depend on the states of recipient patches (i.e., $s_{iX} = s_i$), and that the rates of local extinction do not depend on species identity and patch states (i.e., $e_{iX} = e$).

Equilibrium conditions

It is straightforward to find patch frequencies at equilibria I to IV. To find equilibrium V, we solve

$$s_1 m_1 (1 - p_1) p_1 - e p_1 = 0, \quad (\text{S8a})$$

$$s_2 m_2 (p_1 - p_2) p_2 - 2e p_2 - a p_E = 0, \quad (\text{S8b})$$

$$s_3 m_3 (p_1 - p_3) p_3 - 2e p_3 = 0, \quad (\text{S8c})$$

$$s_2 m_2 (p_3 - p_E) p_2 + s_3 m_3 (p_2 - p_E) p_3 - (3e + a) p_E = 0. \quad (\text{S8d})$$

From (S8a, b, c), we have $p_1 = 1 - e/s_1 m_1$, $p_3 = 1 - (e/s_1 m_1) - (2e/s_3 m_3)$, and

$$p_E = (p_2/a) \{s_2 m_2 (p_1 - p_2) - 2e\}. \quad \text{Noting that } p_1, p_3, \text{ and } p_E > 0, \text{ we have}$$

$$1 - e/s_1 m_1 > 0, \quad 1 - (e/s_1 m_1) - (2e/s_3 m_3) > 0, \text{ and } 1 - (e/s_1 m_1) - (2e/s_2 m_2) > p_2. \quad \text{Noting}$$

also that $p_2 > 0$, we find that $1 - (e/s_1 m_1) - (2e/s_2 m_2) > 0$. Thus, conditions (4), (5),

and (6) are necessary for equilibrium V to be feasible.

Substituting the above expressions for p_1 , p_3 , and p_E into (S8d) yields

$$(p_2 - A)(p_2 + B) = C, \text{ where } A = \{s_1 s_2 m_1 m_2 - e s_2 m_2 - e(a + 2) s_1 m_1\} / s_1 s_2 m_1 m_2,$$

$$B = \{s_1 s_3 m_1 m_3 - e s_3 m_3 + e s_1 m_1\} / s_1 s_2 m_1 m_2, \text{ and } C = e^2 a (2s_2 m_2 + s_3 m_3) / s_2^2 s_3 m_2^2 m_3.$$

Solving this equation for p_2 , $p_2 = \left\{ (A - B) \pm \sqrt{(A + B)^2 + 4C} \right\} / 2$. Noting that $B > 0$ and $C > 0$, we find that one of the solutions, $\left\{ (A - B) - \sqrt{(A + B)^2 + 4C} \right\} / 2$, is always negative. The other solution, $\left\{ (A - B) + \sqrt{(A + B)^2 + 4C} \right\} / 2$, is positive if $AB + C > 0$. This condition yields conditions (7a, b) after rearrangement.

Invasion sequences and coexistence along environmental gradients

Basal productivity

Conditions (4-6) for equilibria I, II, and III are expressed in terms of s_1 as

$$s_1 > \frac{e}{m_1} \equiv s_{1,1}, \quad (\text{S9})$$

$$s_1 > \frac{e}{m_1 \left(1 - \frac{2e}{s_2 m_2} \right)} \equiv s_{1,2}, \quad (\text{S10})$$

$$s_1 > \frac{e}{m_1 \left(1 - \frac{2e}{s_3 m_3} \right)} \equiv s_{1,3}, \quad (\text{S11})$$

where we define a symbol for the right hand side of each inequality, and $s_{1,Y} > 0$ and $s_{1,D} > 0$. In addition, condition (7a) is expressed in terms of s_1 as

$$s_1 < \frac{e}{m_1 \left\{ 1 - \frac{2s_2 m_2 e}{(s_3 m_3)^2} \right\}} \equiv s_{1,a}. \quad (\text{S12})$$

The order of $s_{1,X}$ ($X = B, Y, D, \text{ and } A$) depend on $(s_2 m_2) / (s_3 m_3)$. When $(s_2 m_2) / (s_3 m_3) > 1$, we see that $s_{1,1} < s_{1,2} < s_{1,3} < s_{1,a}$. Thus, with increasing s_1 , the ecosystem becomes invisable to species in the following order: the basal resource ($s_1 > s_{1,1}$), the IG-prey ($s_1 > s_{1,2}$), and the IG-predator ($s_1 > s_{1,3}$). When $s_{1,a} > s_1 > s_{1,3}$, all species can coexist irrespective of a (condition S12). When $s_1 > s_{1,a}$, the coexistence and thus a long food

chain occur only below certain levels of a (condition 7b). When $(s_2m_2)/(s_3m_3) < 1$, we see that $s_{1,1} < s_{1,a} < s_{1,3} < s_{1,2}$. The ecosystem becomes invisable to species in the following order: the basal resource ($s_1 > s_{1,1}$), the IG-predator ($s_1 > s_{1,2}$), and the IG-prey. The levels of s_1 at which the IG-prey can invade the ecosystem depend on a , since the IG-prey can invade the ecosystem only after the IG-predator and where $s_1 > s_{1,a}$.

Disturbance

Conditions (4, 5, 6, 7a) are rewritten in terms of e as follows:

$$e < s_1m_1 \equiv e_1, \quad (S13)$$

$$e < \frac{1}{\frac{1}{s_1m_1} + \frac{2}{s_2m_2}} \equiv e_2, \quad (S14)$$

$$e < \frac{1}{\frac{1}{s_1m_1} + \frac{2}{s_3m_3}} \equiv e_3, \quad (S15)$$

$$e > \frac{1}{\frac{1}{s_1m_1} + \frac{2s_2m_2}{(s_3m_3)^2}} \equiv e_a. \quad (S16)$$

When $(s_2m_2)/(s_3m_3) > 1$, we see that $e_1 > e_2 > e_3 > e_a$. With decreasing e , the ecosystem becomes invisable to species in the following order: the basal resource ($e < e_1$), the IG-prey ($e < e_2$), and the IG-predator ($e < e_3$). When $e_a < e < e_3$, all species can coexist irrespective of a (condition S16). When $e < e_a$, the coexistence and thus a long food chain occur only below certain levels of e (condition 7b). When $(s_2m_2)/(s_3m_3) < 1$, we find that $e_1 > e_a > e_3 > e_2$. The ecosystem becomes invisable to the following order of species: the basal resource ($e < e_1$), the IG-predator ($e < e_2$), and the IG-prey. The levels of e at which the IG-prey can invade the ecosystem depend on a , wince the IG-prey can invade the ecosystem only after the IG-predator and where $e < e_a$.

Ecosystem size

When T is small (i.e., $T < M_1, M_2, M_3$), conditions (4, 5, 6, 7a) are rewritten in terms of T as follows:

$$T > \frac{e}{s_1} \equiv T_1. \quad (\text{S17})$$

$$T > \frac{e}{s_1} + \frac{2e}{s_2} \equiv T_2, \quad (\text{S18})$$

$$T > \frac{e}{s_1} + \frac{2e}{s_3} \equiv T_3, \quad (\text{S19})$$

$$T < \frac{e}{s_1} + \frac{2s_2e}{s_3^2} \equiv T_{a,(123)}, \quad (\text{S20})$$

where we define different symbols for the right-hand sides of inequalities. We assume $M_i > T_j$ ($i, j = 1, 2, 3$), that is, the numbers of propagules produced by a local population of each species are large enough that each species can invade the ecosystem when the ecosystem is large enough. We see that $T_1 < T_2 < T_3 < T_{a,(123)}$ when $s_2/s_3 > 1$, and $T_1 < T_{a,(123)} < T_3 < T_2$ when $s_2/s_3 < 1$. When $s_2/s_3 > 1$, as T increases from below T_1 , the ecosystem can be invaded first by the basal resource ($T > T_1$), then by the IG-prey ($T > T_2$), and by the IG-predator ($T > T_3$). When $s_2/s_3 < 1$, on the other hand, the ecosystem can be invaded first by the basal resource, and then by the IG-predator. Whether the IG-prey can invade the ecosystem where $T > T_2$ depends on a because condition (7a) is not satisfied at $T = T_2$ (see below). To determine the ranges of T that do or do not satisfy condition (7a), we study the sign of $f(T)$, where $f(T) \equiv 1 - e/(s_1m_1) - 2s_2m_2e/(s_3^2m_3^2)$. Condition (7a) is satisfied when $f(T) < 0$, and not when $f(T) > 0$.

Since the functional form of $f(T)$ depends on the size of T relative to M_1, M_2 , and M_3 , we use different symbols to denote different functional forms of $f(T)$ (Table S1). Table S1 lists also the shapes (e.g., monotonic increase or decrease) of $f(T)$ when it takes different

functional forms along the gradient of T . Tables S2-S7 show all possible sequences of the sign of $f(T)$ along the gradient of T . These possible sequences can be determined from the following factors: the order of M_1 , M_2 , and M_3 , the sign of $f(T)$ at $T = M_1$, M_2 , and M_3 , the shapes of different functional forms of $f(T)$, and the existence and locations of real-valued solutions of $f_{(3-12)}(T) = 0$ when $M_3 < T < M_1, M_2$ (proofs are straightforward but lengthy, not shown). In particular, the shapes of different functional forms of $f(T)$ are important to determine the possible sequences. For example, monotonically increasing $f(T)$ changes its sign from minus to plus only once within a range $X < T < Y$ when $f(X) < 0$ and $f(Y) > 0$.