Comments on Theoretical Biology, 7: 257–281, 2002

0894-8550/02 $12.00 + .00
DOI:

A Scrutiny of the Levins Metapopulation Model

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The Levins metapopulation model describes the dynamics of several populations in patches of suitable habitat. These populations may go extinct, leaving empty patches of suitable habitat, but these empty patches may be recolonized by other populations via dispersal. The metapopulation can therefore persist if recolonizations balance local extinctions. This simple model has been criticized for its alleged simplicity, and it has been frequently extended to incorporate more realism. This article scrutinizes the assumptions of the Levins model to reveal its true simplicity. It turns out that many assumptions may be considerably weakened without affecting the model.

Keywords: Conspecific attraction, Levins metapopulation model, rescue effect, separation of time scales, structured models

Albert Einstein once said, "The significant problems we face cannot be solved at the same level of thinking we were at when we created them" (Mayer and Holms, 1996). One such problem is why a patch of habitat is not always occupied by a population of the species for which it is suitable. The Levins (1969, 1970) model solves this problem at a higher level of thinking by introducing the metapopulation concept. A metapopulation is a collection of populations living in discrete patches of suitable habitat. These local

I thank Odo Diekmann for pointing out an inaccuracy in Etienne (2000), Kees Nagelkerke for fruitful discussions about assumption 1, and Hans Heesterbeek for commenting on the manuscript of this article.

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populations may go extinct, for example, due to demographic stochasticity, thus leaving empty patches of suitable habitat, but these empty patches may be recolonized by other local populations via dispersal. Despite local extinctions, the metapopulation can therefore persist if recolonizations balance local extinctions. In such a balance empty suitable habitat is the rule.

The Levins model is generally presented mathematically as

$$\frac{dp}{dt} = cp(1-p) - mp \tag{1}$$

where p is the fraction of habitat patches that are occupied and hence $1-p$ is the fraction of patches that are empty, m is the extinction rate, and c is the colonization rate (see below for a more precise interpretation of c and m). This equation has two equilibria, denoted by p^*. One is trivial equilibrium, $p^* = 0$. The nontrivial equilibrium is given by

$$p^* = 1 - \frac{m}{c} \tag{2}$$

which is only biologically realistic and different from the trivial equilibrium if $c/m > 1$. This condition is also the condition for global stability of the equilibrium. If $c/m \leq 1$, the trivial equilibrium is globally stable. Defining $R_0 = c/m$, one can write the condition for a nontrivial globally stable equilibrium as

$$R_0 > 1 \tag{3}$$

where R_0 is the basic reproduction number and can be interpreted as the expected number of patches colonized during the lifetime of a local population in a virgin environment (i.e., all other patches are empty). If Eq. (3) is satisfied, the local population can more than replace itself before it becomes extinct, and thus the population can grow initially. Because Eq. (2) predicts that p^* is generally smaller than 1, suitable but empty habitat patches are indeed common in a metapopulation.

It is instructive to note that the Levins metapopulation model can be cast in the familiar form of the logistic equation for population growth by writing Eq. (1) as (Amarasekare 1998)

$$\frac{dp}{dt} = rp\left(1 - \frac{p}{K}\right) \tag{4}$$

with

$$r = c - m \tag{5a}$$

$$K = 1 - \frac{m}{c} \tag{5b}$$

An important difference with the logistic model is that the metapopulation carrying capacity is not set beforehand, but it is determined dynamically by the colonization and extinction parameters.

Almost every theoretical text on metapopulations cites this Levins metapopulation model (which Levins himself calls the migration-extinction model in Levins and Culver 1971). According to Hanski (1999) it is one of the three basic models on which all other metapopulation models are grounded; the other two are the two-population model and the lattice model. For example, modifications of the Levins models are the incorporation of rescue effect (Hanski 1983; Hanski et al. 1996; Etienne 2000), patch preference effect (Ray et al. 1991; Etienne 2000) and Allee effect (Amarasekare 1998), and the model concept has been applied to models involving multiple species interactions (Levins and Culver 1971; Slatkin 1974; Sabelis et al. 1991; Hess 1996; Nee et al. 1997; Taneyhill 2000; Gog et al. 2002), succession (Amarasekare and Possingham 2001), heterogeneous habitat (Holt 1997), and the quality of the matrix habitat (Vandermeer and Carvajal 2001), and to structured models containing local population dynamics and dynamics of patch formation and destruction (Hastings 1991, 1995; Gyllenberg and Hanski 1992, 1997; Gyllenberg et al. 1997). While the Levins model is originally a deterministic one, stochastic versions have also been developed (Gyllenberg and Silvestrov 1994; Hanski 1994; Day and Possingham 1995; Vos et al. 2000) of which the spatially explicit incidence function model (IFM) is a particular example tailored to be parameterized by occupancy data. Most of these extended models aim to include more biological realism, because the Levins model itself is often considered overly simplistic, depending on too strong assumptions. It is, however, not always clear what these assumptions are, and how the Levins model is derived from these assumptions. Nor is it always obvious how the parameters in the model should be interpreted. In this article I will try to shed some light on these issues.

THE ASSUMPTIONS OF THE LEVINS MODEL

Hanski and Simberloff (1997), Gyllenberg et al. (1997), and Etienne (2000) list the assumptions that supposedly lead to the Levins model of Eq. (1), while Hastings (1995) lists the assumptions of an extension of the Levins model. From these lists I attempted to build a coherent set of assumptions given below. Often the strong (S) assumptions are made but—as we shall see—the weak (W) assumptions are sufficient and provide more insight.

1S. There are infinitely many patches.
1W. There are sufficiently many patches such that the deterministic approximation is warranted.
2S. Patches are either occupied or empty.

2W1. Local dynamics do not affect colonization and extinction rates.

2W2. Local dynamics occur on a much faster time scale than metapopulation (i.e., colonization–extinction) dynamics, and immigration has no effect on local dynamics.

3. There is no patch structure, that is, they are all alike. In particular there is no spatial structure: Patches are not assigned a specific location in space.
4. Colonization occurs by mass action.
5. There are no correlated extinctions and colonizations.

In this article I focus most attention on the role played by assumptions 1 and 2.

ASSUMPTION 1

Assumption 1W links the deterministic Levins model to its stochastic counterpart with N habitat patches. First I will derive the Levins model from this stochastic model by two methods, one quick and one thorough. The first has as its state variable the probability that a patch is occupied, the second has as its state variable a $(N+1)$-dimensional vector of probabilities that $0, 1, 2, \ldots, N$ are occupied. Then I discuss the implications of assumption 1.

State Variable Is Probability That a Patch Is Occupied

If assumptions 2S, 3, and 5 are made, we can focus on a single patch and describe the dynamics of the probability that it is occupied. Call this probability p; then $1-p$ is the probability that a patch is empty. The rate of change of p is then given by

$$\frac{dp}{dt} = C(p,n)(1-p) - M(p,n)p \tag{6}$$

where $C(p,n)$ is the probability per unit of time that the patch is colonized when empty and $M(p,n)$ is the probability per unit of time that the population in the patch goes extinct when the patch is occupied. They may both depend on p or on the actual number of occupied patches n. The form of Eq. (6) was put forward by Gotelli and Kelley (1993) but they interpreted p as the fraction of occupied patches. For extinction we have $M(p,n) = m$. For colonization we note that assumption 4 implies that $C(p,n)$ must be proportional to n; let us call the proportionality constant c_N. Then Eq. (6) becomes

$$\frac{dp}{dt} = c_N n(1-p) - mp \tag{7}$$

For N large enough (assumption 1W), we can adopt the frequentist interpretation of probability (i.e., the probability of an event can only be inferred from the frequency of occurrence of the event) that the probability of a patch being occupied is equal to the fraction of occupied patches, that is, $p = n/N \Rightarrow n = pN$. Inserting this into Eq. (7) and defining $c := c_N N$ leads to the Levins model of Eq. (1).

State Variable Is Vector with Probabilities of Occupancy

A metapopulation consists of populations like a population consists of individuals. Colonization of empty patches and extinction of populations in a metapopulation are analogous to birth and death of individuals in a population. Let P_n be the probability that n patches out of N are occupied. Following Goel and Richter-Dyn (1974) we can then write down a birth–death model at the metapopulation level:

$$\frac{dP_n}{dt} = C_{n-1}P_{n-1} + M_{n+1}P_n - (C_n + M_n)P_n \tag{8}$$

with

$$P_n = 0 \quad \text{for } n < 0 \text{ and } n > N \tag{9}$$

C_i is the probability of colonization of an empty patch when i patches are occupied and M_i is the probability of local extinction when i patches are occupied. Note that we allow only one extinction event or one colonization event to occur in an infinitesimal time interval. The occurrence of more than one such event is of order dt^2 as long as correlations are absent (assumption 5). For C_n and M_n we have

$$C_n = c_N n(N - n) \tag{10a}$$

$$M_n = mn \tag{10b}$$

where c_N is the colonization probability per unit of time per occupied patch per empty patch and m is the extinction probability per unit of time per occupied patch. This leads to

$$\frac{dP_n}{dt} = c_N(n-1)[N-(n-1)]P_{n-1} + m(n+1)P_{n+1} - [mn + c_N n(N-n)]P_n \tag{11}$$

Multiplying Eq. (11) on both sides by n and summing over all n $(0, \ldots, N)$ gives

$$\begin{aligned}
\sum_{n=0}^{N} n\frac{dp_n}{dt} &= \sum_{n=0}^{N} c_N n(n-1)[N-(n-1)]P_{n-1} + \sum_{n=0}^{N} mn(n+1)P_{n+1} \\
&\quad - \sum_{n=0}^{N} n[mn + c_N n(N-n)]P_n \Longleftrightarrow \\
\frac{d}{dt}\sum_{n=0}^{N} nP_n &= \sum_{i=-1}^{N-1} c_N(i+1)i(N-i)P_i + \sum_{i=1}^{N+1} m(i-1)iP_i \\
&\quad - \sum_{n=0}^{N} mn^2P_n - \sum_{n=0}^{N} c_N n^2(N-n)P_n \\
&= \sum_{n=0}^{N} c_N n^2(N-n)P_n + \sum_{n=0}^{N} c_N n(N-n)P_n + \sum_{n=0}^{N} mn^2P_n \\
&\quad - \sum_{n=0}^{N} mnP_n - \sum_{n=0}^{N} mn^2P_n - \sum_{n=0}^{N} cNn^2(N-n)P_n \\
&= c_N N\sum_{n=0}^{N} nP_n - m\sum_{n=0}^{N} nP_n - c_N\sum_{n=o}^{N} n^2P_n \Longleftrightarrow
\end{aligned}$$

$$\begin{aligned}
\frac{d}{dt}\langle n\rangle &= c_N N\langle n\rangle - m\langle n\rangle - c_N\langle n^2\rangle \\
&= c_N\langle n\rangle[N-\langle n\rangle] - m\langle n\rangle - c_N \mathrm{Var}(n) \Longleftrightarrow \qquad (12a)
\end{aligned}$$

$$\frac{d}{dt}\frac{\langle n\rangle}{N} = c\frac{\langle n\rangle}{N}\left[1-\frac{\langle n\rangle}{N}\right] - m\frac{\langle n\rangle}{N} - c\frac{\mathrm{Var}(n)}{N} \qquad (12b)$$

where we have used that

$$\langle n\rangle = \sum_{n=0}^{n} nP_n \qquad (13a)$$

$$\langle n^2\rangle = \sum_{n=0}^{N} n^2P_n \qquad (13b)$$

From Eq. (12b) we get the Levins model (1) if we set p equal to the expected fraction of occupied patches, that is, $p = \langle n\rangle/N$, and neglect the term involving the variance in n. The deterministic approximation thus comes down to setting the variance of the occupancy equal to 0 when N is large (the simplest form of moment closure). The accuracy of this approximation

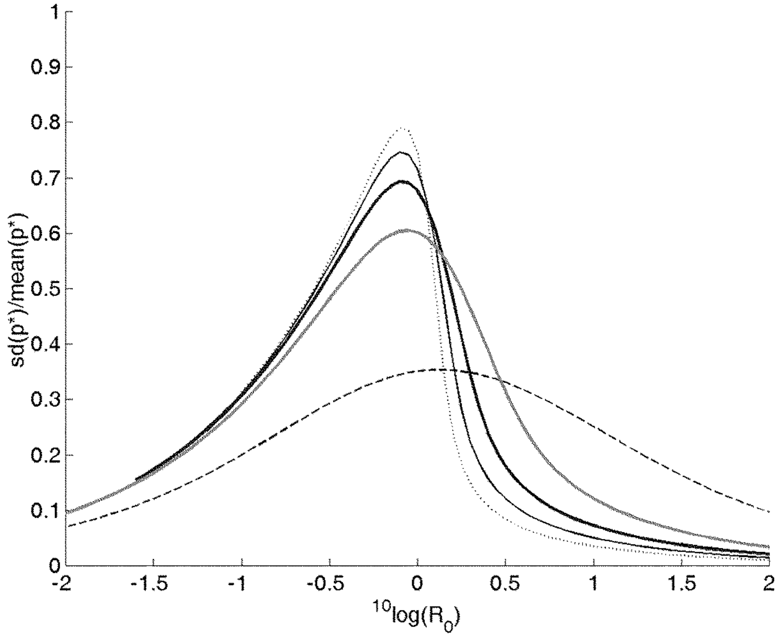

FIGURE 1 Coefficient of variation (standard deviation divided by the mean) of p^* as a function of $R_0 = c_N(N-1)/m$ for different values of N: $N=2$ (dashed), $N=10$ (gray), $N=25$ (solid, thick), $N=50$ (solid, thin), and $N=100$ (dotted).

depends on p and therefore on c_N, N, and m. Figure 1 shows the coefficient of variation as a function of $R_0 = c_N(N-1)/m$ for different values of N when the system is in pseudo-equilibrium, i.e. the stochastic equilibrium conditional on non-extinction. For a fixed value of $R_0 > 1$ the coefficient of variation eventually decreases as N gets larger (note that R_0 also depends on N).

Interpretation

If we take Eq. (12a) and ignore the variance term, thereby effectively setting $\langle n \rangle = n$ where n is the number of patches, we arrive at

$$\frac{dn}{dt} = c_N n(N-n) - mn \tag{14}$$

This form of the Levins model is useful if one wants to study the effect of habitat destruction or creation on metapopulation viability in a deterministic setting, thus excluding stochastic effects for small N.

Traditionally, however, this has been studied by adjusting Eq. (1) slightly to

$$\frac{dp}{dt} = cp(h - p) - mp \tag{15}$$

where h is the fraction of habitat patches that is (still) suitable (Lande 1987; May 1991; Nee and May 1992; Hanski et al. 1996; Hess 1996; Amarasekare 1998; Hanski 1999; Etienne 2000). Equations (14) and (15) are mathematically equivalent but their interpretations are different. Equation (15) is generally (but see Gyllenberg and Hanski 1997) viewed as describing a metapopulation of infinitely many patches according to assumption 1S, so a fraction $h > 0$ of suitable patches still yields an infinite number of suitable patches. If we view the Levins model setting as an infinite surface of equally connected patches, reducing h can be regarded as random patch destruction, which lowers the density of suitable patches on the surface. Equation (15) thus appears to allow for the study of habitat destruction for any $h > 0$ without loss of accuracy of the deterministic approximation, which is certainly appealing. In contrast, Eq. (14) describes a metapopulation consisting of a large but finite number of patches according to assumption 1W. Lowering N reduces both system size (and thereby the accuracy of the deterministic approximation) and patch density. Interestingly, Levins himself used the first interpretation in 1969 (Levins 1969), the second in 1970 (Levins 1970), and both in 1971 (Levins and Culver 1971).

The two interpretations can be linked by rewriting Eq. (15) as

$$\frac{dp}{dt} = c_N N p(h - p) - mp \Leftrightarrow \tag{16a}$$

$$\frac{dn}{dt} = c_N n(Nh - n) - mn \tag{16b}$$

It seems that Eq. (15) can therefore be interpreted as the deterministic limit of the stochastic model with

$$C_n = c_N n(Nh - n) \tag{17}$$

This is true only if we set the total number of patches to Nh because P_n for $n > Nh$ must obviously vanish; Nh now simply plays the role played by N in Eq. (14). We see now that "any $h > 0$" is too bold a statement; we need the additional condition that Nh is sufficient large.

All this only applies (Etienne 2000) if a decrease in h implies that colonists are lost in unsuitable patches that were suitable before. If, somehow, colonists only attempt to colonize suitable patches, a decrease in h has no effect whatsoever in the deterministic model. In the stochastic model, a decrease in h makes the system smaller and thus more vulnerable to chance extinction. However, if decreasing h means decreasing patch density and colonists are subject to mortality during dispersal (e.g., due to predation), such a decrease should be accompanied by a decrease in the colonization probability as well (Hanski and Zhang 1993).

As we saw already, the colonization parameter c in the Levins model (1) in fact depends linearly on N. With assumption 1S, this means that the colonization parameter c_N must be infinitesimally small for c to be a finite number. Stated in a different way, in the Levins model all occupied patches contribute to colonization, and for the total contribution to be finite, their individual contributions must be infinitesimally small. With assumption 1W, the individual contributions are just very small.

ASSUMPTION 2

A frequent obection to the Levins model is that it ignores local dynamics by assuming patches to be either occupied or empty (assumption 2S). Assumptions 2W1 and 2W2 provide the mathematical conditions that local and metapopulation dynamics need to obey to allow for such a simplification as shown below.

Derivation from a Model with Structure in Population Size

We start with assumptions 1S, 3, 4, and 5, so we can clearly focus on assumption 2. Assume that (a) there are n size classes of local populations either measured in number or density, that is, number per unit area, (b) an occupied patch with a local population of class i colonizes empty patches forming a population of class j with rate c_{ij}, and (c) it goes extinct with rate m_i $(i = 1, ..., n)$. Hence, we can have density-dependent colonization and extinction. By a patch of type i we will denote a patch with a population of class i. These patches can change from type i into type j with rate α_{ij} by birth or death ($\alpha_{ii} = 0$). By p_i we denote the fraction of patches with a population of size i. So different patch types only differ in the size of the population they contain, not in, for example, their habitat quality. In other words, the model is still unstructured as far as patches are concerned (assumption 3), but structured as far as local populations are concerned. Because population sizes of all types can be formed by colonization of empty patches, this model is a generalization of the model in Etienne (2000), which is in turn a generalization of Hanski's (1985) model and Hastings's (1991) model that have $N = 2$. I also give a more solid mathematical derivation than Etienne (2000).

The differential equations for the p_i are

$$\frac{dp_i}{dt} = \sum_{j=1}^{n} c_{ji}p_j\left(1 - \sum_{j=1}^{n} p_j\right) + \sum_{j=1}^{n} \alpha_{ji}p_j - \sum_{j=1}^{n} \alpha_{ij}p_i - m_i p_i \qquad (18)$$

$$i = 1, . . . , n$$

Defining

$$p := \sum_{i=1}^{n} p_i \tag{19}$$

and

$$c_j := \sum_{i=1}^{n} c_{ji} \tag{20}$$

we can write down the differential equation for all occupied patches by summing Eq. (18) for all i:

$$\frac{dp}{dt} = \sum_{j=1}^{n} c_j p_j (1 - p) - \sum_{i=1}^{n} m_i p_i \tag{21}$$

because

$$p_1 = p - \sum_{j=2}^{n} p_j \tag{22}$$

the system defined by Eqs. (21) and (18) for all $i > 1$ is equivalent to the system (18) for all i.

Assumption 2W1 implies that colonization and extinction are the same for populations of all sizes: $c_i = c$ for all i and $m_i = m$ for all i. Equation (21) then trivially simplifies to Eq. (1). Assumption 2W1 is biologically very unrealistic, because populations of different sizes generally have different probabilities of colonization and extinction. Fortunately, assumption 2W1 is unnecessarily strong. We just need assumption 2W2. We apply a singular perturbation argument (Tikhonov et al. 1985; for an application see Heesterbeek and Metz 1993). Suppose that local dynamics are much faster than metapopulation processes, that is, the rates α_{ij} on the one hand and the rates c_{ij}, c_j, and m_i on the other hand are at time-scales differing by a factor of $\epsilon \ll 1$. Introducing $\beta_{ij} := \epsilon\alpha_{ij}$ sets the processes at the same time-scale. Multiplying Eqs. (21) and (18) by ϵ leads to

$$\epsilon \frac{dp}{dt} = \sum_{j=1}^{n} \epsilon c_j p_j (1 - p) - \sum_{i=1}^{n} \epsilon m_i p_i \tag{23a}$$

$$\begin{aligned} \epsilon \frac{dp_i}{dt} = {} & \sum_{j=1}^{n} \epsilon c_{ji} p_j \left(1 - \sum_{i=1}^{n} p_j \right) + \sum_{j=1}^{n} \beta_{ji} p_j \\ & - \sum_{j=1}^{n} \beta_{ij} p_j - \epsilon m_i p_i \quad i = 2, \ldots, n \end{aligned} \tag{23b}$$

Let $\tau = t/\epsilon$ represent the fast time-scale. On this scale Eqs. (23a) and (23b) become, after taking the limit $\epsilon \downarrow 0$,

$$\frac{dp}{d\tau} = 0 \tag{24a}$$

$$\frac{dp_i}{d\tau} = \sum_{j=1}^{n} \beta_{ji} p_j - \sum_{j=1}^{n} \beta_{ij} p_i \quad i = 2, \ldots, n \tag{24b}$$

Equation (24a) entails a constant fraction of occupied patches $\tilde{p}$ at the fast time-scale. We can find the quasi-steady state at the fast scale by setting Eq. (24b) equal to 0:

$$\frac{dp_i}{d\tau} = 0 \Rightarrow \tilde{p}_i = \frac{\sum_{j=1}^{n} \beta_{ji} \tilde{p}_j}{\sum_{j=1}^{n} \beta_{ij}} = \frac{\sum_{j=1}^{n} \alpha_{ji} \tilde{p}_j}{\sum_{j=1}^{n} \alpha_{ij}} \quad i = 2, \ldots, n \tag{25}$$

where $\tilde{p}_1 = \tilde{p} - \sum_{j=2}^{n} \tilde{p}_j$ and the tilde denotes the quasi-equilibrium. Equation (25) differs from the equation presented by Etienne (2000) in that the denominator now lacks terms involving m_i because these disappeared in the limits $\epsilon \downarrow 0$. In other words, the m_i were assumed to be negligibly small compared to the α_{ij} and can therefore be omitted. The same argument applies to terms involving c_{ji}. Although we eliminated the equation for p_1, Eq. (25) evidently also applies to $i = 1$. We can therefore write Eq. (25) for all i in matrix notation.

$$\vec{\tilde{p}} = M \vec{\tilde{p}} \tag{26}$$

where

$$\vec{\tilde{p}} = (\tilde{p}_1, \tilde{p}_2, \ldots, \tilde{p}_n)^T \tag{27a}$$

$$M_{ij} = \frac{\alpha_{ji}}{\sum_{j=1}^{n} \alpha_{ij}} \tag{27b}$$

Hence, the quasi-equilibrium $\vec{\tilde{p}}$ is the right eigenvector of the matrix M corresponding to the eigenvalue 1, normalized such that Eq. (19) applies. Let us normalize $\vec{\tilde{p}}$ to unity and denote it by $\vec{q}$. We then have the following expression for $\tilde{p}_i$:

$$\tilde{p}_i = q_i \tilde{p} \tag{28}$$

and hence Eq. (21) turns into

$$\frac{dp}{dt} = c' p(1 - p) - m' p \tag{29}$$

with

$$m' := \sum_{i=1}^{n} m_i q_i \tag{30a}$$

$$c' := \sum_{j=1}^{n} c_j q_j \tag{30b}$$

Thus, the Levins model represents systems of patches with different local population sizes having different extinction and colonization rates, which together lead to effective colonization and extinction rates given by Eqs. (30a) and (30b) as long as local dynamics are faster than metapopulation dynamics. Note that we have not made any special assumptions about the α_{ij} except that they are large compared to c_i and m_i.

Assumption 2W2 also mentions that immigration into already occupied patches is assumed to have no effect on local dynamics. Hanski and Simberloff (1997) state that this follows from the time-scale assumption, so it is not an additional assumption. We argue here to the contrary that it is an additional assumption, by incorporating the immigration effect (called the rescue effect; Brown and Kodric-Brown 1977) into the structured model, and applying the separation of time-scales. Let γ_{ijk} represent the rate at which populations of type i become populations of type j due to colonization from patches with populations of type k; obviously, $\gamma_{ijk} = 0$ for $j \leq i$. Let μ_{ij} represent the rate at which the populations of type i become populations of type j due to emigration out of type i populations; $\mu_{ij} = 0$ for $i \leq j$. The μ_{ij} are related to γ_{ijk}, on which we say more later. Again assuming mass action (assumption 4) for the process of immigration, we have the differential equations

$$\begin{aligned}\frac{dp_i}{dt} = &\sum_{j=1}^{n} c_{ji} p_j \left(1 - \sum_{j=1}^{n} p_j\right) + \sum_{j=1}^{n}\sum_{k=1}^{n} \gamma_{jik} p_j p_k - \sum_{j=1}^{n}\sum_{k=1}^{n} \gamma_{ikj} p_j p_i \\ &+ \sum_{j=1}^{n} \mu_{ji} p_j - \sum_{j=1}^{n} \mu_{ij} p_i + \sum_{j=1}^{n} \alpha_{ji} p_j - \sum_{j=1}^{n} \alpha_{ij} p_i - m_i p_i \quad i = 1, \ldots, n\end{aligned} \tag{31}$$

The same procedure as earlier, with the additional definitions that $\xi_{ijk} := \epsilon\gamma_{ijk}$ and $\nu_{ij} = \epsilon\mu_{ij}$, leads to the following equations at the fast time-scale:

$$\frac{dp}{d\tau} = 0 \tag{32a}$$

$$\begin{aligned}\frac{dp_i}{d\tau} = &\sum_{j=1}^{n}\sum_{k=1}^{n} \xi_{jik} p_j p_k - \sum_{j=1}^{n}\sum_{k=1}^{n} \xi_{ikj} p_j p_i \\ &+ \sum_{j=1}^{n} (\nu_{ji} + \beta_{ji}) p_j - \sum_{j=1}^{n} (\nu_{ij} + \beta_{ij}) p_i \quad i = 2, \ldots, n\end{aligned} \tag{32b}$$

The quasi-steady state at the fast scale follows from setting Eq. (32b) equal to 0:

$$\begin{aligned}\frac{dp_i}{d\tau} = 0 \Rightarrow \tilde{p}_i &= \frac{\sum_{j=1}^{n}\sum_{k=1}^{n} \xi_{jik}\tilde{p}_j\tilde{p}_k + \sum_{j=1}^{n}(\nu_{ji}+\beta_{ji})\tilde{p}_j}{\sum_{j=1}^{n}\sum_{k=1}^{n} \xi_{ikj}\tilde{p}_j + \sum_{j=1}^{n}(\nu_{ij}+\beta_{ij})} \\ &= \frac{\sum_{j=1}^{n}\sum_{k=1}^{n} \gamma_{jik}\tilde{p}_j\tilde{p}_k + \sum_{j=1}^{n}(\mu_{ji}+\alpha_{ji})\tilde{p}_j}{\sum_{j=1}^{n}\sum_{k=1}^{n} \gamma_{ikj}\tilde{p}_j + \sum_{j=1}^{n}(\mu_{ij}+\alpha_{ij})} \quad i = 2,\ldots,n\end{aligned} \tag{33}$$

This is a nonlinear equation in the $\tilde{p}_i$, which can therefore not be put in matrix notation. If for the sake of argument we slightly simplify the equations by assuming that the γ_{ijk} do not depend on the type k of the patch producing the immigrants, that is, $\gamma_{ijk} \equiv \gamma_{ij}$ for all j, then we get

$$\tilde{p}_i = \frac{\tilde{p}\sum_{j=1}^{n}\gamma_{ji}\tilde{p}_j + \sum_{j=1}^{n}(\mu_{ji}+\alpha_{ji})\tilde{p}_j}{\tilde{p}\sum_{k=1}^{n}\gamma_{ik} + \sum_{j=1}^{n}(\mu_{ij}+\alpha_{ij})} \quad i = 2,\ldots,n \tag{34}$$

Realizing that Eq. (34) is now linear and also valid for $i = 1$, it can be cast in the matrix form of Eq. (26) with

$$M_{ij} = \frac{\tilde{p}\gamma_{ji} + \mu_{ji} + \alpha_{ji}}{\tilde{p}\sum_{k=1}^{n}\gamma_{ik} + \sum_{j=1}^{n}(\mu_{ij}+\alpha_{ij})} \tag{35}$$

We can proceed just as in the case without the rescue effect to arrive at a Levins model with adjusted parameters c'' and m'', which are, however, no longer constants but depend on p. In the special case discussed by Etienne (2000), where $n = 2$, $c_{12} = c_{22} = 0$, $c_{11} = c_{21} = c$, $\gamma_{12} = \gamma$, $\mu_{21} = 0$, M is given by

$$M = \begin{pmatrix} 0 & \dfrac{\alpha_{21}}{\tilde{p}\gamma + \alpha_{12}} \\ \dfrac{\tilde{p}\gamma + \alpha_{12}}{\alpha_{21}} & 0 \end{pmatrix} \tag{36}$$

which indeed has an eigenvalue equal to unity with right eigenvector

$$\vec{\tilde{p}} = \begin{pmatrix} \dfrac{\alpha_{21}}{\alpha_{12} + \gamma\tilde{p} + \alpha_{21}} \\ \dfrac{\gamma\tilde{p} + \alpha_{12}}{\alpha_{12} + \gamma\tilde{p} + \alpha_{21}} \end{pmatrix} \tilde{p} \tag{37}$$

and the ODE for p at the slow time-scale is

$$\frac{dp}{dt} = cp(1-p) - \left(m_1 \frac{\alpha_{21}}{\alpha_{12} + \gamma p + \alpha_{21}} + m_2 \frac{\gamma p + \alpha_{12}}{\alpha_{12} + \gamma p + \alpha_{21}} \right) p \tag{38}$$

This result differs from the result in Etienne (2000) in that the fractions in Etienne (2000) contain m_i. This is due to inaccurate application of the time-scale argument in Etienne (2000). As we showed here, the m_i in the fractions must vanish because of the limit $\epsilon \downarrow 0$.

Interpretation

To invoke the time-scale argument we had to assume that c_{ij} and m_i are small compared to the other parameters. This may seem somewhat inconsistent, because m_i can be regarded as a special case of α_{ij} or μ_{ij}, namely, α_{i0} or μ_{i0}. In a similar vein, c_{ij} can be regarded as a special case of γ_{kij}, namely, γ_{0ij}. Hence, the assumption that metapopulation dynamics occur on a slower time-scale than local dynamics entails the assumption of a fundamental difference between colonization of empty patches and population growth due to immigration into occupied patches, and a difference between extinction of a population and population decline due to death and emigration. The first difference can be defended biologically by claiming that colonization of empty patches is hampered by Allee effects and stochastic founder effects, while immigrants into extant populations immediately contribute to population size, thus having a much larger effect. Also, conspecific attraction (Ray et al. 1991; Smith and Peacock 1990; Vos et al. 2000) has a positive effect on immigration but a negative effect on colonization. Yet, for conspecific evasion (e.g., in territorial species; but see Stamps 1991) these effects are reversed. The second difference may be interpreted biologically as a difference between environmental stochasticity or catastrophes causing the entire population to go extinct and demographic stochasticity causing death and emigration of only a few individuals. The former event is rare, while the latter is common. Note also that for the time-scale argument to work mathematically, it is not required that all α_{ij}, μ_{ij}, and γ_{ijk} are large for only one value of j and one value of k must α_{ij} and α_{ij} be large compared to m_i and must γ_{ijk} be large compared to c_{kj}, while there are no conditions at all for μ_{ij}. For example, $j = i + 1$ and $k = n$ reflect that only transitions between adjacent size classes and immigrations from the largest populations are fast.

We can now understand why absence of the rescue effect is often assumed to be implied by the time-scale argument. If metapopulation dynamics is interpreted as including immigration, then the γ_{ijk} are parameters denoting slow processes and thus have no effect on local dynamics. If, however, metapopulation dynamics includes only colonization and extinction, the γ_{ijk} may denote processes at the fast time-scale and induce a rescue effect. In this view, absence of the rescue effect is an independent assumption of the Levins model. Interestingly, I was not fully aware of this myself in Etienne (2000), where I required γ to be small to avoid a conflict with the time-scale argument. We have now seen that this requirement is inconsistent but can easily be avoided.

The parameters c_{ij}, γ_{ijk}, and μ_{ij} are not independent. To gain insight into how they are linked, we separate the dispersal process into three processes: emigration, movement in the matrix between the patches of origin and destination, and immigration (Frank and Wissel 1998; Etienne and Heesterbeek 2000; Ovaskainen 2002). Let d_i^{out} denote the emigration rate out of patches of type i, d_{ik}^{matrix} the probability to survive the journey through the matrix between patches of type i and k (which realistically should depend only on the matrix and not on i and k), and $d_j^{\text{in},k}$ the probability of colonizing (when $k = 0$) or immigration (when $k > 0$) while increasing population size to size class $j > k$ or of decreasing population size to size class $0 < j < k$. Then, examples of expressions for c_{ij}, γ_{ijk}, and μ_{ij} are

$$c_{ij} = d_i^{\text{out}} d_{ik}^{\text{matrix}} d_j^{\text{in},0} \tag{39a}$$

$$\gamma_{ijk} = d_i^{\text{out}} d_{ik}^{\text{matrix}} d_j^{\text{in},k} \tag{39b}$$

$$\mu_{ij} = d_i^{\text{out}} d_j^{\text{in},i} \tag{39c}$$

Thus the mentioned difference between colonization and immigration comes down to a difference between $d_j^{\text{in},k} (j > k > 0)$ and $d_j^{\text{in},0}$. Furthermore, an increase in the emigration rate will result in an increase in all three parameters by the same amount, because more patches undergo these processes. These expressions do not represent the possibility that a larger emigration rate will cause more increases to larger size classes in destination patches and more declines to smaller size classes in the patches of origin, that is, that d_i^{out} affects $d_j^{\text{in},k}$ (all k). For an example of this possibility with $j > k = 0$ see chapter 4 of Etienne (2002).

Derivation from a Model with a Disperser Pool

Splitting up the dispersal process, as in Eq. (39), has led to metapopulation models with a so-called pool of dispersers: Patches produce dispersers, which enter this pool, stay there for some time, and then either die or enter a patch (Gyllenberg and Hanski 1992; Hanski and Gyllenberg 1993; Gyllenberg et al. 1997; Gyllenberg and Metz 2001; Metz and Gyllenberg 2001). We follow the model of Hanski and Gyllenberg (1993), which consists of an ODE for the population size x, a PDE for the fraction of patches p with population size x and carrying capacity y (which are continuous quantities in contrast to the discrete quantities in the models presented earlier), and an ODE for the dispersers D and a boundary condition for the PDE:

$$\frac{dx(t)}{dt} = g(x, y) - \gamma(x, y) + \alpha\psi(y)D(t) \tag{40a}$$

$$\frac{\partial}{\partial t}p(t,x,y) + \frac{\partial}{\partial x}\left[\frac{dx(t)}{dt}p(t,x,y)\right] = -m(x,y)p(t,x,y) \tag{40b}$$

$$\frac{dD(t)}{dt} = -(\alpha + v)D(t) + \int_1^\infty \int_1^\infty \gamma(x,y)p(t,x,y)\,dx\,dy \tag{40c}$$

$$\begin{aligned}&[g(1,y) - \gamma(1,y) + \alpha\psi(y)D(t)]p(t,1,y)\\ &\qquad = \beta(y)D(t)\left[h(y) - \int_1^\infty p(t,x,y)\,dx\right]\end{aligned} \tag{40d}$$

where $g(x,y)$ describes population growth (for example, as a logistic equation), $\gamma(x,y)$ is the emigration rate (which we called d_i^{out} in the model with discrete size classes earlier), α describes the rate at which dispersers leave the pool and arrive at some patch, $\psi(y)$ is the probability of arriving at a patch of carrying capacity y that reflects patch quality (similar to $d_j^{\text{in},k}$), $m(x,y)$ is the extinction rate as before, v is the mortality rate during dispersal (which was reflected in d_{ik}^{matrix}), $\beta(y)$ describes the per disperser and per empty patch rate at which dispersers colonize empty patches successfully (similar to $d_j^{\text{in},0}$), and $h(y)$ is the fraction of patches of carrying capacity y. This model incorporates assumptions 1S, 4, and 5, but relaxes assumptions 2 and 3 by allowing population size to have an effect on colonization and extinction, and by allowing patches of different quality.

Hanski and Gyllenberg (1993) derive the Levins model as follows. All patches have equal quality (assumption 3), hence $h(y) = \delta(y - y_0)$, that is, the Dirac measure concentrated at the carrying capacity y_0. Furthermore, β, γ, and m are independent of population size x (assumption 2W1, see later discussion). With the definition, similar to (19), $p(t) := \int\int p(t,x,y)\,dy\,dx$, model (40) reduces to two ODEs:

$$\frac{dp(t)}{dt} = \beta D(t)[1 - p(t)] - mp(t) \tag{41a}$$

$$\frac{dD(t)}{dt} = -(\alpha + v)D(t) + \gamma p(t) \tag{41b}$$

Hanski and Gyllenberg (1993) then say that the assumption that local dynamics are much faster than metapopulation dynamics (first part of assumption 2W2, see later discussion) makes the rates α, v, and γ much larger than β and m, which then leads to

$$D(t) = \frac{\gamma}{\alpha + v} \tag{42}$$

Inserting this in Eq. (41a) gives (1) with colonization rate c''' defined by

$$c''' := \frac{\beta\gamma}{\alpha + v} \tag{43}$$

Interpretation

Hanski and Gyllenberg (1993) thus apply the time-scale argument in a different way than Etienne (2000). They state that Eq. (42) follows from the assumption that local dynamics are much faster than metapopulation dynamics, but in fact they assume disperser dynamics (emigration, mortality, and immigration) to be much faster than metapopulation dynamics (colonization and extinction). In addition, they applied a stronger assumption when they set the rates β, γ, and m independent of population size. This is just assumption 2W1.

At the same time, the assumption that disperser dynamics are much faster than metapopulation dynamics was actually also made to get Eq. (32b). There we required that γ_{ijk} be much larger than c_{ij} and m_i, and γ_{ijk} consists of the ingredients d_i^{out}, d_{ik}^{matrix}, and $d_j^{\text{in},k}$ as exemplified in Eq. (39b), which are akin to, respectively, γ, ν, and α of the model of Hanski and Gyllenberg (1993). So we must interpret local dynamics in assumption 2W2 as all processes different from colonization and extinction.

ASSUMPTION 3

I discuss two extensions of the Levins model that relax assumption 3. The first allows patch quality to differ between patches, and the second allows patches to have a specific spatial location.

A Model with Structure in Patch Quality

While structure in population size does not affect the form of the Levins model as long as metapopulation dynamics are slow enough relative to other processes, structure in patch quality can no longer be represented by a single Levins-type ODE. Gyllenberg and Hanski (1997) describe such a model where patch quality is either discrete or continuous. Suppose assumptions 1S, 2S, 4, and 5 are made. Let $c(x)$ and $m(x)$ be the colonization rate and extinction rate, respectively, of a local population in a patch of quality x, and let $h(dx)$ be the measure denoting the fraction of patches with quality x: this measure notation allows patch quality to be either discrete $[h(dx) = h_x,\ x = 1, \ldots, \infty]$ or continuous $[h(dx) = h(x)\,dx]$ or both (e.g., a point mass h_1 at $x = 1$, and a continuous density $h(x)$ for $x > 1$). In the same vein $p(dx)$ is the measure denoting the fraction of occupied patches of quality x.

Gyllenberg and Hanski prove that if

$$\int_{(0,\infty)} \frac{c(x)}{m(x)} h(dx) > 1 \tag{44}$$

there is one globally stable nontrivial equilibrium, given by

$$p^* = \int_{(0,\infty)} \frac{C^*}{C^* + m(x)} h(dx) \tag{45}$$

with C^* satisfying

$$\int_{(0,\infty)} \frac{c(x)}{C^* + m(x)} h(dx) = 1 \tag{46}$$

while $p^* = 0$ if Eq. (44) is violated. If all patches have equal quality (assumption 3), then $h(dx) = \delta(x - x_0)dx$ and Eq. (44) reduces to $c(x_0)/m(x_0) > 1$, which is equivalent to Eq. (3), and Eq. (45) reduces to $p^* = 1 - m(x_0)/c(x_0)$, in which we recognize Eq. (2).

Thus, although this model is not reducible to the Levins model with adjusted parameters as before, it possesses the same properties as the Levins model. In this sense, the Levins model can be claimed to be even robust to relaxation of assumption 3 as far as patch quality is concerned.

A Model with Spatial Structure

Suppose assumptions 1W, 2S, 4, and 5 hold. Let p_i describe the probability that a patch at location i is occupied. For this patch we can write the equivalent of Eq. (6),

$$\frac{dp_i}{dt} = C_i(p,n)(1 - p_i) - M_i(p,n)p_i \tag{47}$$

We now follow Ovaskainen and Hanski (2001), who define

$$M_i(p,n) = \frac{m}{w_i} \tag{48a}$$

$$C_i(p,n) = c_N \sum_{j \neq i}^{N} s_{ij} p_j \tag{48b}$$

where w_i and s_{ij} do not depend on the p_i, and m and c_N are species-specific parameters (see also Adler and Nuernberger 1994 and Hanski and Ovaskainen 2000). Let M be a matrix with elements $M_{ij} = w_i s_{ij}$ for $j \neq i$ and $M_{ii} = 0$. Ovaskainen and Hanski (2001) show that there is a globally stable nontrivial equilibrium, if and only if

$$\frac{c_N}{m} \lambda_M > 1 \tag{49}$$

where λ_M is the dominant eigenvalue of M. With the following weighted version of Eq. (19)

$$p_\lambda^* = \sum_{i=1}^{N} l_i r_i p_i^* \tag{50}$$

where l_i and r_i are the ith components of the left and right leading eigenvectors of the matrix with elements $(c_N/m)M_{ij}(1 - p_i^*)$ scaled such that $\Sigma_{i=1}^{N} l_i r_i = 1$, the nontrivial equilibrium p_λ^* can be written as (Ovaskainen et al. 2002)

$$p_\lambda^* = 1 - \frac{m}{c_N \lambda_M} \tag{51}$$

Comparing Eq. (49) with Eq. (3) and Eq. (51) with Eq. (2) we see that the spatially structured Levins model has exactly the same properties as the original Levins model, which thus turns out to be even robust to relaxation of assumption 3 as far as spatial structure is concerned.

Interpretation

The realm of the Levins model now appears to be almost endless. Its basic properties are still conserved when we relax the assumption that there is no structure in patch quality or patch location. However, as far as spatial structure is concerned, this has only been shown for functions $M_i(p, n)$ and $C_i(p, n)$ as in Eq. (48). And these functions deserve scrutiny themselves. The rate C_i at which patch i is colonized, see Eq. (47), depends on the occupancy of the patches (occupied or empty) at time t, and not on the probabilities of occupancy p_i at time t. Assumption 1W offers no help now; we cannot use the frequency interpretation of probability, because $n_i = 1$ for all i—that is, each patch is at a unique location. Ovaskainen and Hanski (2001) do not provide a mathematical or biological justification for Eq. (48b).

It is interesting to draw a parallel between the spatially structured model and the Levins model given by Eq. (7). For equally sized patches with equal interpatch distance, λ_M is given by the number of patches N. Hence, λ_M can be regarded as a properly weighted measure of the capacity of the landscape to contain a metapopulation. It was therefore termed the metapopulation capacity (Hanski and Ovaskainen 2000).

ASSUMPTION 4

Assumption 4 states that colonization is proportional to the product of the patches of origin and the patches of destination. In the Levins model, these are the occupied patches and the empty patches; in the model with rescue effect the occupied patches are also patches of destination. In the model structured by population size, there are patches of origin and of destination for each population size class. Assumption 4 should not be interpreted as stating that the choice of patches by potential colonists is random, which I show in an example.

A Model with Conspecific Attraction

Ray et al. (1991) introduced a conspecific attraction parameter A, which is the probability (or degree) that a disperser will look for other occupied patches with conspecifics where it will then settle. Such dispersers are wasted from a metapopulation point of view because colonization of already occupied patches has no effect on metapopulation persistence (assuming no rescue effect). In this case, choice of patches by potential colonists is clearly nonrandom.

The dynamics are described by

$$\frac{dp}{dt} = cp(1-p)(1-A) - mp \tag{52}$$

which is equivalent to Eq. (1) with $c'''' := c(1-A)$. Thus, the Levins model also covers conspecific attraction as long as the random part of colonization occurs by mass action (and the nonrandom part has no effect on metapopulation dynamics). The model is, however, mathematically fully equivalent to a model in which a fraction A of the potential dispersers stay in their patch, so colonization is simply reduced. This can also be interpreted biologically as conspecific attraction being one of the causes for dispersal.

In the model of Ray et al. (1991), a fraction A of the dispersers will not settle in empty patches, even if there are no occupied patches at all other than the patch where they are produced. Conspecific attraction can then hardly be the cause for dispersal. It may be easier to consider conspecific attraction as acting on dispersers that have already left their patch of origin.

Suppose that the total number of colonizations of both occupied and empty patches per unit of time is cp. Assume further that $c_1 p^2$ is the number of colonizations of occupied patches per unit of time and $c_2 p(1-p)$ is the total number of colonizations of empty patches per unit of time. Hence, we have mass action for all processes, but with different proportionality constants. The relative value of c_1 to c_2 is a measure of the amount of conspecific attraction. We must have

$$c_1 p^2 + c_2 p(1-p) = cp \tag{53}$$

This can only be true for all p if c_1 and/or c_2 depend on p, which violates assumption 4. An example of such a model is given in Etienne (2000) where

$$c_1 = \frac{c\frac{1}{v}}{1-p+\frac{p}{v}} \quad \text{and} \quad c_2 = \frac{c}{1-p+\frac{p}{v}}$$

with $v = c_2/c_1$ denoting the preference for empty patches relative to the preference for occupied patches.

ASSUMPTION 5

Although the importance of correlated colonizations and extinctions has been acknowledged (Harrison and Quinn 1989; Gilpin 1990; Akçakaya and Ginzburg 1991; Sutcliffe et al. 1997; Frank and Wissel 1998; Etienne and Heesterbeek 2001; Ovaskainen et al. 2002), they have scarcely been studied in the context of the Levins model. Correlated extinctions in particular may have a large impact on metapopulation persistence. I show how relaxation of assumption 5 in a special case of such correlated extinctions still allows for a Levins model with rescaled extinction parameter.

Derivation From the Stochastic Birth–Death Model

Suppose assumptions 2S, 3, and 4 are satisfied. Let mN denote the probability per unit of time that a disaster occurs; this reflects the idea that a larger number of patches N will usually cover a larger area with a corresponding larger risk of disasters occurring. Let r_k denote the probability that a disaster affects k patches, wiping out the extant population when a patch is occupied and having no effect when a patch is empty; if $r_k > 0$ for some $k > 1$ then correlated extinctions may occur. We must require $\sum_{k=1}^{N} r_k = 1$. Furthermore, let $Q_{ij}(k)$ denote the probability that the disaster affecting k patches reduces the number of occupied patches from i to j. Assuming that empty and occupied patches are equally likely to be affected, $Q_{ij}(k)$ is hypergeometrically distributed, that is,

$$Q_{ij}(k) = \frac{\binom{i}{j}\binom{N-i}{N-k-j}}{\binom{N}{N-k}} \tag{54}$$

With these assumptions, Eq. (11) becomes

$$\frac{dP_n}{dt} = c_N(n-1)[N-(n-1)]P_{n-1} + mN\sum_{k=1}^{N}\sum_{j=1}^{k} r_k Q_{n+j,n}(k)P_{n+j} - \left[mN\sum_{k=1}^{N}\sum_{j=1}^{k} Q_{n,n-j}(k) + c_N n(N-n)\right]P_n \tag{55}$$

I consider the special case that $r_k = 0$ for $k > 2$ here and explore the full model elsewhere. The two extinction terms of Eq. (55) sum to

$$m\left[(n+1)\left(r_1 + 2r_2\frac{N-1-n}{N-1}\right)P_{n+1} + (n+1)r_2\frac{n+2}{N-1}P_{n+2}\right.$$
$$\left.-n\left(r_1 + 2r_2\frac{N-n}{N-1} + r_2\frac{n-1}{N-1}\right)P_n\right] \tag{56}$$

Multiplying by n, summing, and using some algebra similar to that required in Eq. (12), gives $-m(1+r_2)\langle n\rangle$. Inserting this into Eq. (12a) and applying assumption 1W results in

$$\frac{d}{dt}\langle n\rangle = c_N\langle n\rangle[N - \langle n\rangle] - m'''\langle n\rangle \tag{57}$$

with

$$m''' = m(1+r_2) \tag{58}$$

We see that the Levins model also represents systems with correlated extinctions, at least in this special case where only two populations can go extinct at the same time; the extinction rate is merely increased by a factor $1 + r_2$ where r_2 is the probability that a disaster affects two patches.

CONCLUSION

In this article I have examined the assumptions of the Levins model. Many of the assumptions that are often considered unrealistic can be relaxed without affecting the model; Eq. (1) remains applicable, albeit with rescaled parameters. In other words, the parameters in Eq. (1) represent many mechanisms, including local dynamics, correlated extinctions and one form of conspecific attraction. Furthermore, even in cases where simple parameter rescaling does not suffice, the properties of the Levins model (a nontrivial equilibrium for p if $R_0 > 1$) remain intact when spatial structure and patch quality are incorporated. At the same time, there are certainly important mechanisms that the Levins model does not describe, notably the rescue effect, a second form of conspecific attraction, and the extensions listed in the introduction. Careful examination of a model's assumptions is therefore absolutely necessary to know the model's action radius.

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