A Unifying Framework for Metapopulation Dynamics

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Abstract: Many biologically important processes, such as genetic differentiation, the spread of disease, and population stability, are affected by the (natural or enforced) subdivision of populations into networks of smaller, partly isolated, subunits. Such “metapopulations” can have extremely complex dynamics. We present a new general model that uses only two functions to capture, at the metapopulation scale, the main behavior of metapopulations. We show how complex, structured metapopulation models can be translated into our generalized framework. The metapopulation dynamics arising from some important biological processes are illustrated: the rescue effect, the Allee effect, and what we term the “antirescue effect.” The antirescue effect captures instances where high migration rates are deleterious to population persistence, a phenomenon that has been largely ignored in metapopulation conservation theory. Management regimes that ignore a significant antirescue effect will be inadequate and may actually increase extinction risk. Further, consequences of territoriality and conspecific attraction on metapopulation-level dynamics are investigated. The new, simplified framework can incorporate knowledge from epidemiology, genetics, and population biology in a phenomenological way. It opens up new possibilities to identify and analyze the factors that are important for the evolution and persistence of the many spatially subdivided species.

Keywords: metapopulation, rescue effect, multiple equilibria, Allee effect, antirescue effect.

The spatial structure of a population can profoundly affect genetic, epidemiological, and population dynamic processes within that population. For example, subdivision of a population can influence gene flow and enhance the rate of loss of genetic diversity in subpopulations (Lacy 1987; Pannell and Charlesworth 1999), which sometimes results in harmful levels of inbreeding (Sacceri et al. 1998). However, spatial subdivision is also a requirement for beneficial local adaptations to occur (Rolán-Alvarez et al. 1997; Joshi et al. 2001). Within epidemiology, the rate of contact between subpopulations crucially influences the development of a disease outbreak (Grenfell and Harwood 1997). Population biologists have found a wide variety of cases where spatial structure influences the stability of single- and multispecies systems, both in nature and in theoretical settings (Tilman and Kareiva 1997; Hanski 1999). All the processes exemplified above also have the potential to affect the viability or extinction risk of single subpopulations. An appreciation of spatial influences on biological processes has proven important for the understanding of basic evolutionary and ecological phenomena. This appreciation is also urgently needed if we are to improve the management of the many endangered species living in fragmented habitats.

However, the construction and analysis of mathematical models of spatially structured populations has turned out to be a formidably complicated task. The processes within a subpopulation can be as complex as in an ordinary single population and are, in addition, intricately affected by the dynamics of neighboring patches via the migration of individuals. Impressive efforts have been made to model such “metapopulations,” taking into account the size, growth rate, and age structure of each subpopulation (Levins 1969; Hastings and Volin 1989; Allen et al. 1993), patch quality (Hanski 1994), matrix quality (Vandermeer and Carvajal 2001), correlated random events (Harrison and Quinn 1989), and interactions with predators (Taylor 1990; Holt 1997). A few models have even attempted to predict the dynamics of real-world metapopulations (Hanski 1994). These detailed, so-called structured models are necessary to describe specific populations or specific processes. Unfortunately, as the models describe specific situations and populations with increasing accuracy, they inevitably grow in complexity and have been found to be unsuited for establishing general principles concerning metapopulation dynamics: “This general framework, however, leads to a class of models that are typically too complex to analyze” (Hastings and Harrison 1994, p. 175).
"Although limited mathematical analysis is possible, ... it is hard to extract many useful ecological results and predictions without making some further simplifying assumptions" (Hanski 1999, p. 64).

Simplified models are needed to address general questions in biology that concern the whole metapopulation scale. However, the simple metapopulation models that have been available, Levins's (1969) model and variants thereof, are too restricted (Gyllenberg et al. 1997). As we will show in this study, this is because they do not allow for a range of biological phenomena affecting the dynamics of metapopulations at the metapopulation level. While a good general model does not have to include all details of the real world to give interesting insights, it should be able to express the dynamics of the system, at the level it attempts to capture (Caswell 1988). While it has been argued that the shortcomings of the unstructured Levins model stem from its many unrealistic assumptions about the local dynamics of subpopulations (Burgman et al. 1993; Hanski and Zhang 1993), we show that the limitations are instead at the description of the metapopulation-level processes themselves. We use the vital core of Levins’s model to build a new phenomenological model that is unstructured but nonetheless captures much more of the dynamic flexibility of metapopulations.

The new model is used to visualize and classify the metapopulation dynamics that can arise from different main types of extinction and colonization processes. We show how structured models can be incorporated into our simplified framework, making it easier to understand the origin of their behavior. Finally, we give an example on how extinction times of small metapopulations are influenced by the assumed shape of the colonization and extinction functions.

About Levins’s Model

Richard Levins introduced a new approach to the study of patchy populations (Levins 1969). In his model he assumes that the environment is composed of $T$ identical habitat patches. Patches are classified as either occupied or empty; there is no additional local structure. Occupied patches send out emigrants at rate $m$, and these migrants colonize unoccupied patches. Occupied patches go extinct with the rate $e$. When the two processes of extinction and colonization counterbalance there is an equilibrium number of occupied patches. The characterization of equilibria is important since natural metapopulations are expected, and are sometimes also found, to move toward such “equilibria of patch occupancy” (Hanski 1999).

However, in Levins’s model, it is assumed that the arrival of a migrant at an empty patch always turns that patch into an occupied patch. Thus, the colonization rate of each patch in Levins’s model is preset; it increases proportionally with the number of patches occupied ($N$). Consequently, total colonization rate in the whole metapopulation ($C$) is given by $C = mN(1 - N/T)$. Further, Levins’s model assumes the extinction rate per patch to be a constant, independent of the number of surrounding occupied patches. Thus, the total extinction rate ($E$) in a Levins-type metapopulation is preset to just increase linearly as the number of occupied patches increases: $E = eN$.

As we will demonstrate, these preset functions ($C$ and $E$) leave out important biological processes that act at the metapopulation scale and are the reasons why Levins’s model cannot act as a good phenomenological model for metapopulations. In order to capture the dynamics of metapopulations, we must allow for different types of dependencies between migration and colonization rates and between migration and extinction rates. This is because per patch colonization rate can differ systematically from the assumed function of Levins’s model; for example, it might take several individuals to establish a new subpopulation so that the colonization rate can have a nonlinear dependence on migration rate (see “Allee Effect” and “The Effects of Differential Migration”). Also, the influx of migrants can significantly affect the subpopulation extinction rate. This effect can be positive (e.g., by the demographic contribution of immigrants to small populations) or negative (e.g., by the introduction of a lethal disease); see “Rescue Effect” and “Antirescue Effect.” We develop a framework that can embrace most of the relevant metapopulation-level processes (i.e., those that affect patch occupancy).

A Generalized Metapopulation Model

Faithful to the classic metapopulation scenario of Levins (1969), we let the environment be composed of $T$ discrete patches, where at any given time each patch is either occupied or not. Each occupied patch sends out successful migrants at rate $m$. (By “successful” migrants, we mean those that survive to reach another patch.) However, in contrast to traditional patch-occupancy models, we will not assume specific shapes of the functions for the rates at which patches are colonized ($C$) or go extinct ($E$). And, importantly, we shall allow for the possibility that the extinction rate is influenced by the rate of immigration. We define two general functions, the colonization rate per patch $C_{\text{patch}}(\alpha)$ and the extinction rate per patch $E_{\text{patch}}(\beta)$, where $\alpha$ denotes the rate of arrival of colonizers onto an unoccupied patch and $\beta$ denotes the rate at which immigrants arrive at an occupied patch. We assume that these arrival rates for immigrants are functions $\alpha(N)$ and $\beta(N)$ of the number of occupied patches ($N$). The rate at
which empty patches are colonized in a metapopulation
according to this new generalized framework is given by

$$C_{total}(N) = (T - N)C_{patch} \alpha(N).$$  \hfill (1)$$

The rate at which occupied patches switch to empty
patches $E_{total}(N)$ in the new framework is

$$E_{total}(N) = NE_{patch} \beta(N).$$  \hfill (2)$$

These two functions (eqs. 1, 2) are the core of the
new flexible model. By allowing for various dependencies
between extinction and colonization on migration we now
can account for most metapopulation-level dynamics. To
find the rate at which the number of occupied patches
changes with time in the metapopulation, we make the
same deterministic approximation to the stochastic change
in $N$ as is made in Levins’s model. That is, we assume that
the number of patches is large enough to make stochastic deviations in $N$
insignificant. Then the rate of change in
patch occupancy is given by

$$\frac{dN}{dt} = C_{total}(N) - E_{total}(N).$$  \hfill (3)$$

The immigration rates $\alpha(N)$ and $\beta(N)$ could be different and
have a complex dependence on the number of occupied
patches, $N$. However, for ease of exposition, we assume
that migrants settle at random so that $\alpha = \beta = mN/T$. This assumption will be relaxed later. Setting
$\alpha(N) = mN/T$ in equation (1), we obtain

$$C_{total}(N) = T(1 - x)C_{patch}(mx),$$

where $x = N/T$ denotes the proportion of occupied patches. Similarly, setting $\beta(N) = mN/T$ in
equation (2), we obtain

$$E_{total}(N) = TxE_{patch}(mx).$$

Since $dN/dt = Tdx/dt$, equation (3) now reduces to

$$dx/dt = f(x),$$

where

$$f(x) = (1 - x)C_{patch}(mx) - xE_{patch}(mx).$$  \hfill (4)$$

When extinction and colonization rates counterbalance,
we have an equilibrium proportion of occupied patches ($x^*$). At equilibrium we have $dx/dt = 0$, so that $x^*$ satisfies

$$f(x^*) = 0.$$  \hfill (5)$$

If $f(x^*) < 0$, the equilibrium is stable, and the metapopulation will deterministically return to the equilibrium after a small perturbation. If $f(x^*) > 0$, the equilibrium is unstable and a small perturbation away from the equilibrium will either make the metapopulation move
toward another equilibrium of patch occupancy or cause metapopulation extinction. We will now look at the meta-
population dynamics that arise from several different types of biologically interesting colonization $C_{patch}$ and extinction functions $E_{patch}$. However, we first look at the traditional
Levins model again. We will repeatedly return to this
model, but as a specific, basic case of the generalized framework.

**Levins’s Functions Rewritten**

In Levins’s model the arrival of an immigrant at an un-
occupied patch changes that patch into an occupied patch. This can be written as

$$C_{patch}(\alpha) = K\alpha$$

in our generalized model, where the constant $K$ is the proportion of immigrants arriving at an unoccupied patch that succeed in establishing an occupied patch. The total colonization rate

$$C_{total}(N)$$

in the metapopulation thus satisfies

$$\frac{C_{total}(N)}{T} = \left(1 - \frac{N}{T}\right)Km \frac{N}{T} = (1 - x)Kmx.$$  \hfill (5)$$

Levins’s model assumes the patch-specific extinction rate to be $E_{patch}(\beta) = e$, where $e$ is a constant, which gives

$$\frac{E_{total}(N)}{T} = \frac{eN}{T} = xe.$$  \hfill (6)$$

Equation (4) becomes

$$f(x) = (1 - x)Kmx - xe = x(Km - e - Kmx).$$  \hfill (7)$$

Thus, the preset shapes of the functions limit Levins’s model to the single equilibrium $x^* = 1 - e/Km$. Because $f(x^*) < 0$, the equilibrium is stable. The well-known dy-
namics of Levins’s model is visualized in figure 1. An equilibrium point occurs where the colonization rate
equals the extinction rate (fig. 1A). It can be seen that for
any given value of the migration rate ($m$) the two functions intersect only once (fig. 1B). A higher migration rate al-
ways implies a higher patch occupancy ($N/T$) at equilib-
rium in Levins’s metapopulation scenario. Below we will illustrate what happens with the dynamics of metapopu-
lations for a range of examples when migration has a
different influence on subpopulation extinction and
establishment.

**Rescue Effect**

The demographic contribution of migrants to small dw-
inding subpopulations may reduce subpopulation extinction risk—the “rescue effect” (Brown and Kodric-Brown
1977). Logically, if all subpopulations are of the same size
and have the same migration rate (as assumed in Levins’s
model), there will be no rescue effect, since subpopulations
will lose as many (or more) migrants as they gain. There-
fore, the rescue effect has primarily been included in more
complex models (Gyllenberg et al. 1997; but see Hanski
Figure 1: Metapopulation dynamics for Levins’s classic metapopulation model showing the dependence of the colonization rate (\(C\)) and extinction rate (\(E\)) on the proportion of occupied patches (\(N/T\)). The proportion of occupied patches is in equilibrium when \(C = E\), that is, when the colonization and extinction function intersect. When the migration parameter \(m\) is small, the colonization and extinction function do not intersect (except at 0) and there is no equilibrium at which the population is not extinct. When the migration parameter \(m\) is sufficiently large, they intersect once and there is a unique stable equilibrium. \(A\), \(C\), and \(E\) illustrated for \(m = 0.5\). \(B\), Colonization rate (white surface) and extinction rate (dark surface) as functions of the proportion of occupied patches (\(N/T\)) for a range of migration parameter \(m\). Equations (5) and (6) with \(e = 0.2\) and \(K = 1.0\). (Concerning the range of migration rates \([m]\) that are illustrated in figs. 1–6, the absolute value of \(m\) can be rescaled by rescaling the time, so it has no significance in the figures. In contrast, \(Km/e\) is dimensionless, and its absolute value is critical in determining metapopulation properties.)

To illustrate this type of mechanism, we assume the colonization function of Levins (eq. [5]) but take

\[
E_{\text{patch}}(\beta) = \frac{e}{1 + A\beta}
\]

(where \(A\) is a positive constant), so that \(\beta\) has a strong positive effect at low values. The result of this generalized rescue effect is to bend the extinction planes in figures 1A and 1B until those in figures 2A and 2B are obtained. If a stable metapopulation size is possible in Levins’s model (the current model with \(A = 0\)), then including the rescue effect (\(A > 0\)) simply increases the stable size. However, if Levins’s model predicts the metapopulation would go extinct (\(Km < e\)), a stable metapopulation size can still exist when a rescue effect is present. And, interestingly, if there is such a stable size, then it can be shown that there must be a second, smaller, unstable metapopulation size as well (fig. 2A). This phenomenon of multiple equilibria in patch...
occupancy has earlier been described in more complex models only (Gyllenberg et al. 1997).

Metapopulation dynamics depend crucially on the form of the relationship between the immigration rate and the reduction in extinction risk. For example, a linear decreasing extinction risk, $E_{\text{patch}}(\beta) = e - A\beta$, has only one equilibrium. In contrast, for threshold populations, extinction rate may be little affected by immigration rate while this rate is small but may drop rapidly once a threshold immigration rate is reached (May 1977). To illustrate this mechanism, consider this case:

$$E_{\text{patch}}(\beta) = \frac{e}{1 + A\beta}.$$  

For this function the metapopulation has three equilibria for some values of $e$ and $m$ (fig. 3). When three equilibria occur, two stable equilibria are separated by an unstable equilibrium. For low patch occupancy the rescue effect is weak and the model is similar to Levins’s model. Thus, when $e$ is slightly smaller than $Km$, there is a stable equilibrium at low patch occupancy. As patch occupancy increases above a threshold, the rescue effect takes hold and the extinction rate plummets below the colonization rate, resulting in one unstable and a second stable equilibrium at higher patch occupancy.

### Antirescue Effect

The literature on metapopulations has largely ignored detrimental effects of immigration that are well known from epidemiology and genetics. An increased extinction rate with increasing immigration rate, the “antirescue effect,” might be due to immigrants carrying parasites or diseases (Grenfell et al. 1995; Grenfell and Harwood 1997) or gene flow reducing local adaptation (Hastings and Harrison 1994; Rolán-Alvarez et al. 1997; Joshi et al. 2001; see box 1A). A high migration rate can also cause synchronous fluctuations in local population sizes, which increases the extinction risk for the whole metapopulation (Allen et al. 1993; Burgman et al. 1993; Schöps 1999; box 1B). Although our framework cannot explicitly handle these processes, it can capture the main effect at the metapopulation level by allowing local extinction risk to increase with immigration rate (fig. 4). Consider a case where the colonization rate is as in Levins’s model (eq. [5]) but the per patch extinction function is increasing in $\beta$.

### Box 1: Increased Migrations Can Increase Extinction Risk

**A.** The periwinkle, *Littorina saxatilis*, has different ecotypes living in different microhabitats, just a few meters apart. Attacks from crabs favor large, ridged shells in the upper shore, whereas heavy wave action promotes small, smooth shells at the lower shore. The two morphs and their hybrid survive equally well along a narrow zone of intermediate habitat (Rolán-Alvarez et al. 1997). The parental morphs as well as hybrids have very low survival if transplanted to a nonnatal microhabitat. Interestingly, gene flow between the two morphs is strongly reduced by the combination of nonpelagic larvae and assortative matings (Rolán-Alvarez et al. 1997). Thus, a low migration rate and assortative mating strongly promote the locally adapted genotypes that are crucial to periwinkle survival in different microhabitats.

**B.** A New Zealand weevil. A metapopulation of the weevil *Hadramphus spinipennis* inhabits steep, partly isolated creeks along the shores of two islands in New Zealand. The subpopulations of weevils overexploit the host plant and have frequent, asynchronous local extinctions (Schöps 1999). The distribution area of the host plant was dramatically increased after a deforestation of the islands. The increased connectivity between subpopulations increased the local extinction rates. Future survival of *H. spinipennis* depends on a maintained low connectivity between subpopulations (Schöps 1999).
Allee Effect

In Levins’s model the arrival of an immigrant at an unoccupied patch changes that patch into an occupied patch. This is generalized to \( C_{\text{patch}}(\alpha) = K\alpha \) in our model. However, colonization rate need not be proportional to immigration rate. For example, it may be difficult initially to establish subpopulations because of demographic, stochastic, or genetic complications at low population numbers—the “Allee effect” (Allee 1931). Consider the S-shaped colonization function \( C_{\text{patch}}(\alpha) = \alpha\beta(\alpha + \beta) \), where \( \beta \) is a constant (as earlier used in a structured model by Hanski [1994]) and \( C_{\text{patch}}(\beta) = e \). At the metapopulation level, the most important consequence of this change in the colonization function is that there can be two equilibria of patch occupancy (fig. 5). If patch oc-
cupancy is below \( N^*_i \), extinction rate exceeds colonization and the population rapidly goes extinct. Above \( N^*_i \) and below the higher equilibrium \( N^*_e \) colonization rate exceeds extinction rate, and the patch occupancy will increase until \( N^*_i \) is reached (fig. 5A). Other similar S-shaped colonization functions give the same qualitative results.

The Effects of Differential Migration

So far we have assumed that migrants settle on a patch chosen at random. Migrants may, however, avoid patches that are already occupied in order to avoid competition for territories or food. Alternatively, migrants seeking a mate, or those at risk from predation while alone, may try to settle on already occupied patches. When there is such differential migration, the rate of arrival of potential colonizers is no longer given by \( \alpha(N) = mN/T \), and this will change how colonization rate depends on \( N \). To investigate the effect of differential migration, we take the per patch colonization and extinction rates to be \( C_{\text{patch}}(\alpha) = K \alpha \) and \( E_{\text{patch}}(\beta) = e \), respectively, as in Levins’s model. Note this means that \( C_{\text{patch}}(\alpha(N))/N \) does not depend on \( N \) when \( \alpha(N) = mN/T \).

Consider first the extreme case when migrants avoid occupied patches and each settles on an empty patch chosen at random. Then \( \alpha(N) = mN/(T - N) \) and hence

\[
\frac{C_{\text{total}}(N)}{T} = K m e.
\]  

(12)

If \( Km < e \), then the metapopulation goes extinct as in Levins’s model. If \( Km > e \), then at the unique equilibrium all patches are occupied. In reality, differential migration is not likely to be this extreme, particularly since not all migrants will be able to find an unoccupied patch when these are rare. Different degrees of this “repellent behavior” will produce different colonization functions, but all have steeper initial increase and result in higher equilibrium patch occupancies \( (N/T) \) than the symmetrical colonization function of Levins’s model.

Now suppose that migrants seek occupied patches. In the extreme case in which there is no immigration to unoccupied patches, there is no colonization, and the population will go extinct. Suppose instead that migrants settle on an unoccupied patch if they do not soon encounter an occupied patch. Then \( \alpha(N)/N \) will be a decreasing function of \( N \). Thus, the function \( C_{\text{patch}}(\alpha(N))/N \) will be decreasing in \( N \). This is in contrast to models in which there is an Allee effect and no differential migration, where \( C_{\text{patch}}(\alpha(N))/N \) is an increasing function of \( N \). In this sense there is an “anti-Allee effect” when migrants seek occupied patches.

We can also consider the effect of differential migration on the extinction rate. When migration rate affects per-patch extinction rate, as happens when there is a rescue or antirescue effect, differential migration will interact with these effects to distort the extinction function \( E_{\text{total}}(N) \). For example, suppose that the patch extinction rate increases with immigration rate as a result of the spread of disease. Then extinction rate will be lowest when few patches are occupied. Suppose that migrants also try to avoid occupied patches. Since they will be most successful at doing so when few patches are occupied, the extinction rate will be further reduced when few patches are occupied but could be little affected when most patches are occupied. Thus, in this example, the differential migration would accentuate the antirescue effect in the metapopulation even more.

Translating Structured Models

Metapopulation models in which local populations have structure appear fundamentally more complex than our generalized metapopulation model. However, as the following example shows, they can be translated into our much simpler framework while still preserving the important metapopulation-scale features.

Let us first consider a simple structured metapopulation model that has been developed to study metapopulations where immigration positively affects local populations, increasing population density and reducing population extinction risk. Thus, this is a model designed to capture the rescue effect (Hanski 1985; see also Hanski and Gyllenberg 1993; Hanski 1999). Assume that patches are in one of three states: empty (state 0), low population (state 1), or high population (state 2). A low-population patch transforms into a high-population patch at rate \( r_l(\alpha) \), where \( \alpha \) is the rate at which it receives immigrants. A high-population patch changes to a low-population patch at rate \( r_h(\alpha) \). We assume that \( r_l(\alpha) \) is an increasing function of \( \alpha \) and \( r_h(\alpha) \) is a decreasing function. A patch in state \( i \) (\( i = 1, 2 \)) sends out migrants at rates \( m_i \). We assume that \( m_i < m_2 \). A patch in state \( i \) (\( i = 1, 2 \)) changes into an empty patch at rate \( e_i \). We assume \( e_1 > e_2 \). An empty patch changes into a low-population patch at rate \( Ke \).

We now assume that extinction and colonization rates, \( e_i, e_j, \) and \( K \alpha \), are small compared with the rates \( r_i \) and \( r_j \). (Later we comment on the case when this approximation does not hold.) Then the proportion of occupied patches that are of each type can be assumed to equilibrate before there is a change in the number of occupied patches due to a colonization or extinction event. Specifically, let there be \( N \) occupied patches, of which a proportion \( p \) are high population. Then the rate at which patches receive immigrants is


\[ \alpha = \frac{N[(1 - \rho)m_1 + \rho m_2]}{T}. \]  

(13)

Thus, ignoring colonization and extinction events, at equilibrium the rates at which high- and low-population patches convert to one another are equal,

\[ Npr_2(\alpha) = N(1 - \rho)r_1(\alpha). \]  

(14)

Eliminating \( \alpha \) from equations (13) and (14) gives the equilibrium proportion of occupied patches that are high population, \( \rho(N) \). Our assumptions about the dependence of \( r_1(\alpha) \) and \( r_2(\alpha) \) on \( \alpha \), and that \( m_1 < m_2 \), guarantee that \( \rho(N) \) is an increasing function of \( N \). The total patch extinction rate in the metapopulation is then

\[ E_{total}(N) = N[1 - \rho(N)]e_1 + \rho(N)e_2 \]

\[ = N[e_1 + \rho(N)(e_2 - e_1)], \]  

(15)

and the total colonization rate is

\[ C_{total}(N) = (T - N)KN\frac{[(1 - \rho(N))m_1 + \rho(N)m_2]}{T} \]

\[ = (T - N)KN\frac{[m_1 + \rho(N)(m_2 - m_1)]}{T}. \]  

(16)

These two functions are illustrated in figure 6. In this model, colonization of empty patches is as in Levin's model, and the extinction rate of a patch of a given type does not depend on the immigration rate into that patch. Thus, at the microscopic level there is no rescue effect or Allee effect. However, at the macroscopic level the model exhibits both effects (fig. 6). To see this, first focus on the average per patch extinction rate:

\[ \frac{E_{total}(N)}{N}. \]  

(17)

This is a constant function of \( N \) in Levin's model. It decreases as \( N \) increases when there is a rescue effect, and it increases with \( N \) when there is an antirescue effect. In our structured model \( \rho(N) \) is an increasing function of \( N \). Thus, by equation (15), \( \frac{E_{total}(N)}{N} \) is decreasing in \( N \) (since it is assumed that \( e_2 < e_1 \)). In other words, at the macroscopic level, our structured model exhibits a generalized rescue effect. Now consider the function

\[ \frac{C_{total}(N)}{(T - N)N}. \]  

(18)

In Levin's model this is constant, whereas it is increasing in \( N \) when there is an Allee effect. In our structured model, equation (16) shows that the function (18) is increasing in \( N \) (since it is assumed that \( m_1 < m_2 \)). This is synonymous with a pronounced Allee effect at the macroscopic level (cf. figs. 5A, 6A). The tendency of this model to produce two equilibria thus stems from generalized rescue and Allee effects. The dynamics of this type of model have earlier been claimed to stem from a rescue effect only (Hanski 1985, 1999; Hanski and Gyllenberg 1993). Thus, the simplified framework presented here can be used to avoid confusion about the origin of the dynamics of structured metapopulation models.

The above method, by which a structured metapopulation leads to an unstructured analogue with the same metapopulation-level dynamics, is easily generalized (see next paragraph). To make this translation it is assumed that colonization and extinction occur on a slower timescale than local subpopulation dynamics. When this timescale assumption is not met the detailed population dy-
namics of the structured metapopulation model and our unstructured analogue will no longer agree. However, if the goal is to determine the equilibria of a structured metapopulation, the approach outlined above is still valid. This is because, at an equilibrium of a metapopulation, time-scales are not important since the system is stationary. Thus, the unstructured analogue, which assumes fast local dynamics, has the same equilibria as the original structured metapopulations with slow local dynamics.

More Complex Structured Models

The above approach, in which a three-state model is translated into an unstructured model, generalizes to more complex models as follows. Suppose that there are a total of $T$ patches and that the population on a patch may be of the $I + 1$ types $0, 1, 2, \ldots, I$, where type 0 corresponds to the patch being empty. The other states can describe different patch sizes or actual local population sizes. As in our example, we assume that patch dynamics is fast relative to colonization and extinction rates. The number of occupied patches then determines the proportion $p_i(N)$ that are type $i$. Let a type $i$ population contribute migrants to a pool at rate $m_i$. Then the total rate at which migrants enter the pool is $Nm(N)$, where

$$m(N) = \sum_{i=1}^{I} p_i(N)m_i.$$  \hfill (19)

If pool members settle on patches at random, the rate at which unoccupied patches receive immigrants is $\alpha = m(N)N/T$. Assuming that the colonization rate of an empty patch is $C_{\text{patch}}(\alpha)$, we have

$$\frac{C_{\text{total}}(N)}{T} = (1 - x)C_{\text{patch}}(\alpha m(N)),$$  \hfill (20)

where $x = N/T$. Let a type $i$ population ($i = 1, \ldots, I$) become extinct at rate $e_i$. Then the extinction rate is $E_{\text{total}}(N) = NE_{\text{patch}}(N)$, where

$$E_{\text{patch}}(N) = \sum_{i=1}^{I} p_i(N)e_i.$$  \hfill (21)

Thus, a structured model (with constant extinction probability for given structure) can be replaced by the generalized Levins-type model with no structure but a migration-rate-dependent extinction risk.

Finite Patch Numbers

So far we have assumed that the total number of patches ($T$) is large. It has also been implicitly assumed that colonization and extinction events at one location occur independently of what occurs at other patch locations (given the current $N$). It is then reasonable to treat colonization and extinction events as occurring at a smooth rate. Metapopulation dynamics are consequently deterministic, and a metapopulation that reaches a stable equilibrium will remain there indefinitely. Conservation theory is, however, often concerned with the vulnerability to extinction of metapopulations that are subject to stochastic effects (Tilman et al. 1994; Hill and Caswell 2001). The details of how stochasticity operates are then crucial to questions of metapopulation persistence (Lande et al. 1998). For example, there might be large-scale fluctuations in weather conditions that affect all patches in a highly correlated way (Harrison and Quinn 1989). Alternatively, patches could be independent as in our deterministic model, with the stochasticity due to the low number of patches (Hanski 1999; Hill and Caswell 2001). We do not attempt a full analysis of the effects of stochasticity in this article. Instead, we illustrate the effects of stochasticity in this latter alternative.

When $T$ is low, the actual events of extinction and colonization become important. Suppose $N$ patches are currently occupied. Before, the functions $C_{\text{total}}(N)$ and $E_{\text{total}}(N)$ were interpreted as rates. Now we assume that the time to wait for the next patch colonization (given no extinction occurs before then) is an exponentially distributed random variable with parameter $C_{\text{total}}(N)$. Similarly, the time to wait for the next extinction (given no colonization occurs before then) is an exponentially distributed random variable with parameter $E_{\text{total}}(N)$. These two random variables are assumed to be independent. Under these assumptions the time for the number of occupied patches to change has an exponential distribution with mean $\tau(N) = [C(N) + E(N)]^{-1}$. After the change, the number of occupied patches is $N + 1$ with probability $p(N) = C(N)/(C(N) + E(N))$ and is $N - 1$ with probability $1 - p(N)$.

Figure 7 illustrates the use of this stochastic version of our generalized model. The figure shows how the mean time to population extinction depends on the total number of patches in the environment. In each of the four cases shown, we have kept the colonization function as in Levins’s model. The extinction functions presented are for two different cases of the rescue effect and a case with the antirescue effect, together with the baseline Levins case for comparison. When there is an antirescue effect, the mean time to extinction is only substantially reduced when the detrimental effect of increased immigration is very strong.
(as in the case shown). This is because the antirescue effect is strongest when there are many patches occupied, and extinctions matter least. When the per patch extinction rate drops rapidly once immigration rates reach a threshold (eq. [9]), there is a stable equilibrium comparable with that in the Levins case and a second stable equilibrium at a higher proportion of occupied patches. As a result, the mean time to extinction is very much above that for Levins’s model, especially when the total number of patches is small. In contrast, the advantage of a rescue effect of the form given by equation (8) has its strongest effect when the total number of patches is large (fig. 7).

Discussion

By stochastic necessity, all populations will eventually go extinct, and this is true in particular for small populations. The persistence of a metapopulation that is divided into a network of smaller subunits is dependent not only on the local development within single subpopulations but also on the overall picture of how many new habitat patches are colonized each year, compared with the number of subpopulations that go extinct. The metapopulation concept introduced by Levins acknowledges this fact by focusing solely on the rates of colonizations and extinctions (Levins 1969). However, Levins assumed a fixed shape of the colonization function and also assumed extinction rate to be a per patch constant. Thereby, Levins’s model became unable to express the effects of many biological processes that affect metapopulation dynamics.

Many processes influencing metapopulation dynamics have their origin in local processes of subpopulations and are linked to migration. We have mentioned processes such as local genetic adaptations, inbreeding, demographic contributions, and epidemics. They all act at the local scale, are mediated via migrations, and can have a profound impact on the whole metapopulation (its patch occupancy and/or its persistence). As is evident from the examples above, the expected influence from migration on subpopulation persistence and metapopulation dynamics can be very different among metapopulations. The new framework presented here allows for any functional relationship between migrations and colonization rates and between migrations and extinction rates. Therefore, although the new model does not explicitly describe processes operating at the subpopulation scale, it captures their metapopulation-level effects.

We have sampled the literature for examples of different functional relationships for C and E on migration rate. With the appropriate choice of functions, the new model can incorporate the effects of different colonization patterns. Some populations have problems establishing colonies at low population sizes and are increasingly successful at higher immigration rates. This is allowed for by the hill-like colonization function in the Allee effect (Allee 1931; Hanski 1994; fig. 5). Also, differential migration behavior of individuals can lead to an Allee effect at the metapopulation level (if individuals prefer empty patches) or to an anti-Allee effect (if individuals prefer already occupied patches). Further, by allowing the extinction function to vary with migration rate the new model describes how immigration affects existing subpopulations. The extinction function can describe beneficial effects, such as demographic contribution of immigrants and prevention of inbreeding via gene flow with different types of rescue effects (figs. 2, 3). However, the rate of extinctions can increase with increased migration rates. Examples of deleterious effects of immigration are the spread of disease and the loss of local adaptation via gene flow. We term the general phenomenon of harmful effects of increased immigration on local extinction risk the antirescue effect (fig. 4).

The actual functions given in this article are to be regarded as examples of “main type functions” used to illustrate the phenomenology of how different processes affect overall metapopulation dynamics. For implementation on specific questions, the appropriate C and E functions must be found. After mean extinction and colonization rates have been derived from a natural population, or from a complex model, our model can describe the meta-
population-scale dynamics in a transparent and easily analyzed way. This makes it possible to classify and compare the main behaviors of completely different complex systems.

So what can we expect the C and E functions to be like in real-world metapopulations? We believe it can be useful to consider how the metapopulation has been formed. Many populations live on “naturally” patchy habitats. Habitats can be networks of rock pools, islands, the intestines of birds, or, as a more unusual example, the sunken carcasses of whales (T. Dahlgren, unpublished manuscript). We suggest that species evolved in such systems can be expected to have developed optimal dispersal strategies related to the benefits and risks of migrations in their environments. Another type of patchy population is artificially created. Modern farming and forestry have changed the main vegetation of entire landscapes, leaving only scattered patches of the once dominant vegetation types left. Species that have inhabited larger, unbroken habitats for perhaps thousands of generations might not have optimal dispersal strategies to cope with the new constraints imposed by a sudden fragmentation of their habitats.

The focus of metapopulation research has been directed toward endangered species, living on small remnants of their natural habitat. Those populations are likely to benefit from increased migration rates to counteract their imposed isolation. Consequently, a rescue effect is included in most metapopulation models investigating conservation issues (such as habitat loss). However, it is important to rule out other functional relationships since high migration rates can be detrimental for some populations (e.g., by inducing synchronous fluctuations in local populations [Vandermeer and Carvajal 2001] or by loss of genetic diversity [Lacy 1987; Pannell and Charlesworth 1999]). The antirescue effect highlights this possibility in a phenomenological way (fig. 4). Two examples where extinction risk increases as migration rate increases are the periwinkle (Rolán-Alvarez et al. 1997; box 1A) and a New Zealand weevil (Schöps 1999; box 1B). Studies of metapopulations with antirescue effects can give insights into the evolution of nondispersal strategies, for example, site fidelity, winglessness, and territoriality. The awareness of how colonization and extinction functions affects metapopulation dynamics. Our article advocates such a study.

For some studies, the desired general C and E functions for a specific biological process can be found by first building a structured model, which then is reduced to our simplified model. The simplified model can capture the essential detail, at the metapopulation level, of the structured metapopulation model. Once such a simplified model has been constructed, the dependence of the colonization and extinction functions affects metapopulation dynamics. Our article advocates such a study.

Earlier extensions of Levins’s model that tried to make it more realistic added a linear rescue effect to Levins’s model to take into account demographic contribution from migration (Hanski 1982, 1985). Also, Gotelli and Kelly (1993) suggested that C and E could be any function of N; however, they only explored the linear rescue effect. The linear rescue effect gives only one stable equilibrium of patch occupancy. The dynamic limitations of Levins’s model and these extensions with linear rescue effect were believed to be an inherent property of all unstructured metapopulation models: “The most fundamental difference between the unstructured and structured metapopulation models is that with the structured models there can be multiple equilibria” (Gyllenberg et al. 1997, p. 107; see also Hanski and Gyllenberg 1993). Consequently, the use of simple Levins-type models in analyzing general questions such as consequences of patch destruction on metapopulation persistence (Tilman et al. 1994) has been criticized (Gyllenberg et al. 1997). We show that a simple model can express most of the complex behaviors described for structured metapopulation models by varying the different functional relationships between migration, colonization, and extinction rates. Although there have previously been specific simple extensions to Levins’s model, there has been no attempt to systematically investigate how the form of the colonization and extinction functions affects metapopulation dynamics. Our article advocates such a study.
lags into our unstructured analogue. Studies that address specific processes (such as influence from explicit spatial location, time since colonization, and genotype frequencies), must obviously utilize more complex models allowing for these parameters to be estimated. The generalized model is designed to capture processes that leave a signature at the metapopulation scale.

The generalized model presented here can be used as a phenomenological model in the study of general aspects of metapopulation structure. Interesting areas for theoretical applications are environmental stochasticity and extinction risks for metapopulations with different types of colonization and extinction functions, evolution of optimal migration rates, time-lagged responses in patch occupancy, and investigation of the implicit assumptions of more complex models.

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