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Long-Distance Rescue and Slow Extinction Dynamics Govern Multiscale Metapopulations

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ABSTRACT: Rare long-distance dispersal is known to be critical for species dynamics, but how the interplay between short- and long-distance colonization influences regional persistence in a fragmented habitat remains poorly understood. We propose a metapopulation model that combines local colonization within habitat islands and long-distance colonization between islands. We study how regional occupancy dynamics are affected by the multiscale colonization process. We find that the island size distribution (ISD) is a key driver of the long-term occupancy dynamics. When the ISD is heterogeneous—that is, when the size of islands is variable—we show that extinction dynamics become very slow. We demonstrate that this behavior is unrelated to the well-known extinction debt near the critical extinction threshold. Hence, this finding questions the equivalence between extinction debt and critical transitions in the context of metapopulation collapse. Furthermore, we show that long-distance colonization can rescue small islands from extinction and sustain a steady regional occupancy. These results provide novel theoretical and practical insights into extinction dynamics and persistence in fragmented habitats and are thus relevant for the design of conservation strategies.

Keywords: spatial ecology, habitat fragmentation, population persistence, short- and long-distance colonization, island size distribution, extinction debt, Griffiths phase.

Introduction

Habitat fragmentation influences population dynamics and species distributions in many ecosystems (Fahrig 2003). A key issue is whether species are able to survive in local populations and colonize remote sites that are suitable for establishment. Colonization is the foundation of new populations based on the successful establishment of dispersing propagules or individuals. Therefore, colonization depends on species dispersal capabilities. Understanding and predicting species dynamics in a fragmented habitat is the central motivation of metapopulation theory (Hanski and Gaggiotti 2004). This theory considers the balance between colonization of unoccupied suitable sites and extinction of existing populations.

Designing metapopulation models with realistic colonization functions depending on the ability of organisms to send successful individuals and propagules into remote suitable habitats is a major challenge (Oborny et al. 2005; Baguette et al. 2013). Although for many organisms biological constraints favor short-distance dispersal of propagules, some studies have shown that long-distance dispersal events, even if rare, can strongly influence species dynamics over the long term (Clark 1998; Bonte et al. 2010). These dispersal abilities then determine both the spatial extent of local populations (Cavanaugh et al. 2014) and the connectivity of remote areas through colonization events (Baguette 2003; Hovestadt et al. 2011; Andrello et al. 2013). Therefore, the relative importance of short- and long-distance colonization is a key issue both for defining correctly the nodes and edges of a metapopulation network (Fletcher et al. 2013) and for addressing its long-term dynamics (Hiebeler 2004). Metapopulation models were first designed under the assumption of uniform colonization across the metapopulation (Levins 1969), and efforts have been devoted ever since to introduce more realistic colonization functions and variation in population sizes (Etienne 2000; Ovaskainen and Hanski 2001). However, how the combination of frequent short-distance and rare long-distance colonization events influences metapopulation persistence has been rarely addressed in these models (Hiebeler 2004).

In this article, we investigate the relative influence of short- and long-distance colonization on regional metapopulation dynamics and species persistence in a fragmented habitat. Characterizing habitat fragmentation is a challenging issue, and multiscale patterns of aggregation are often observed (Bolliger et al. 2003). For simplicity,

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habitat structure is often represented by a network of local patches of varying sizes so that the connectivity between patches depends on species' colonizing abilities (Hanski and Ovaskainen 2000). This description is oversimplified because each patch is assumed to include a single population, and the habitat between patches is assumed to be strictly unsuitable for population establishment. The patch definition is to be relaxed to account for population and habitat structure beyond the patch limits (e.g., Cavanaugh et al. 2014). In addition, multiscale habitat clustering generates structural heterogeneity in the metapopulation network. A fragmented habitat can be seen, in first approximation, as a set of islands composed of well-connected local populations, while populations belonging to different islands are poorly connected, a property called modularity (Andrello et al. 2013). We thereby propose here a multiscale framework of metapopulation including three basic levels (fig. 1): (i) local populations in habitat sites where demographic equilibrium is instantly attained but can become extinct with a given probability, (ii) habitat islands containing submetapopulations depending on the balance of extinction and short-distance colonization within the islands, and (iii) a regional set of habitat islands characterized by an island size distribution (ISD) where long-distance dispersal allows for colonization between islands. We study how the metapopulation dynamics are affected by such multiscale spatial structures as those observed in real habitats (Bolliger et al. 2003).

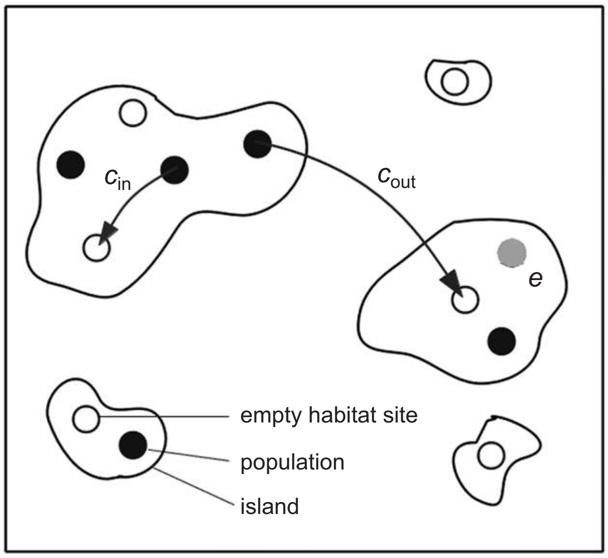

Figure 1: Multiscale metapopulation model. The habitat consists of a set of islands. Each island contains a submetapopulation. A habitat site in an island can be occupied by a population (filled circle) or be empty (open circle). The parameters defining the metapopulation dynamics are the extinction rate for one population, e; the within-island colonization parameter, c_{in}; and the long-distance colonization parameter, c_{out}. The gray circle represents a population that is becoming extinct.

Our basic hypothesis is that the relative importance of within- and between-island colonization and the heterogeneity of island sizes critically influence metapopulation dynamics. Without dispersal between islands, the populations within an island form a finite-sized (sub)metapopulation governed by stochastic dynamics (Ovaskainen 2001; Etienne and Nagelkerke 2002). These submetapopulations ultimately become extinct, and their extinction times are known to strongly depend on island size. In particular, for a regional metapopulation with islands of different sizes, smaller islands become extinct before larger ones. This leads to a sequence of submetapopulation extinctions, which can generate nonintuitive dynamics leading toward extinction on the regional scale, especially if the ISD is strongly heterogeneous. We hypothesize that these sequential extinction dynamics are much slower than those for a homogeneous ISD, in which island sizes are all equal. Furthermore, we will argue that these slow dynamics are not related to any critical transition. Hence, this behavior is fundamentally different from the slow-dynamics regime expected at the critical extinction threshold of a classical metapopulation, which has been conceptualized as "extinction debt" (Tilman et al. 1994; Dakos et al. 2011). Therefore, we argue that the scope of the extinction debt concept should be enlarged beyond the context of critical transitions, which has been given the most attention in both theoretical and applied research. In addition, we study whether and how long-distance colonization affects this behavior. We expect that when dispersal between islands is strong enough, large islands that survive longer become sources of colonizers that sustain persistence in the smaller islands, which would become extinct otherwise. We call this behavior "regional rescue" and thereby extend the concept of local population rescue (Gotelli 1991) to the context of a realistic multiscale fragmented habitat. We describe the conditions under which the multiscale metapopulation exhibits (quasi)stationary persistence and slow extinction dynamics according to these expectations. Our model opens perspectives for addressing both ecological and evolutionary issues on species dynamics and dispersal strategies.

Material and Methods

Multiscale Habitat Structure

We consider a habitat network consisting of an infinite number of islands, each including a finite number of sites. We denote the fraction of islands in the network with n sites by $P(n)$, which defines the ISD. We have $\sum_n P(n) = 1$, and the mean island size $\bar{n}$ is given by $\bar{n} = \sum_n nP(n)$.

The analysis of the metapopulation model below holds for any ISD. We illustrate the results using a flexible family of ISDs, combining a power law dependence with exponent β and an exponential dependence with characteristic size γ (for details, see app. A; apps. A–D are available online). The two parameters β and γ allow us to control the mean $\bar{n}$ and the variance σ^2 of the ISD.

We thereby study how $\bar{n}$ and σ^2 affect the metapopulation dynamics. Our hypothesis is that island size heterogeneity critically influences occupancy dynamics. Therefore, we compare our model dynamics for a heterogeneous ISD (variance: $\sigma^2 > 0$) with the corresponding homogeneous ISD (variance: $\sigma^2 = 0$), that is, the ISD in which all islands have size $\bar{n}$. Throughout the article, we use the homogeneous ISD as a reference case.

Multiscale Metapopulation Dynamics

Our metapopulation model describes the colonization-extinction dynamics of populations at habitat sites. The populations belonging to a habitat island form a submetapopulation where short-distance colonization events occur. Each submetapopulation is coupled to the submetapopulations of other islands through long-distance colonization (fig. 1). The regional metapopulation is composed of the overall set of submetapopulations in habitat islands. We are interested in how the heterogeneity of island sizes generates complex stochastic dynamics in the regional metapopulation.

At a given time, each habitat site is either occupied by a population or empty. We denote by $p_k^{(n)}$ the probability that k sites are occupied in an island of size n. Hence, the average fraction $f^{(n)}$ of occupied sites in islands of size n is given by

$$f^{(n)} = \sum_{k=1}^{n} \frac{k}{n} p_k^{(n)}, \tag{1}$$

and the average fraction f of occupied sites in the regional metapopulation is given by

$$f = \sum_n \frac{nP(n)}{\sum_m mP(m)} f^{(n)} = \sum_n \frac{nP(n)}{\bar{n}} f^{(n)}. \tag{2}$$

When an extinction event occurs, the state of a habitat site changes from occupied to empty. We denote by e the extinction rate for one population. The probability that a specific population becomes extinct in a small time interval δt is thus equal to $e\delta t$. Conversely, when a colonization event occurs, the state of a habitat site changes from empty to occupied. Our model considers two possible sources of colonizers: an occupied site within the same habitat island and an occupied site of another island. For colonization from within the island, we consider that the colonization rate of empty sites is proportional to the fraction of occupied sites in the island and to the number of empty sites available for colonization in the island. Hence, for an island of size n with k occupied sites, the rate of colonization of empty sites from the populations of the island is

$$c_{\text{in}} \frac{k}{n}(n-k), \tag{3}$$

where c_{in} is the within-island colonization parameter.

Similarly, for colonization from another island, we assume that the colonization rate of empty sites is proportional to the fraction of occupied sites in the entire habitat and to the number of empty sites available for colonization in the recipient island. Hence, for an island of size n with k occupied sites, the rate of colonization from another island is

$$c_{\text{out}} f(n-k), \tag{4}$$

where c_{out} is the long-distance colonization parameter. For the sake of realism, we assume that long-distance colonization is much less frequent than local colonization, that is, $c_{\text{out}} \ll c_{\text{in}}$.

On the basis of the extinction and colonization processes, the number of occupied sites k in an island of size n can undergo the following transitions:

$$\begin{aligned} &k \rightarrow k+1 \quad \text{with rate} \quad \lambda_k = c_{\text{in}} \frac{k}{n}(n-k) + c_{\text{out}} f(n-k), \\ &k \rightarrow k-1 \quad \text{with rate} \quad \mu_k = ek. \end{aligned} \tag{5}$$

These transitions determine the dynamics of the probability $p_k^{(n)}$ that k sites are occupied in an island of size n:

$$\frac{\mathrm{d}p_k^{(n)}}{\mathrm{d}t} = \lambda_{k-1} p_{k-1}^{(n)} + \mu_{k+1} p_{k+1}^{(n)} - \lambda_k p_k^{(n)} - \mu_k p_k^{(n)}. \tag{6}$$

The first (second) term of the right-hand side corresponds to a transition from $k-1$ to k (from $k+1$ to k) occupied sites, increasing the probability $p_k^{(n)}$. The third (fourth) term corresponds to a transition from k to $k+1$ (from k to $k-1$) occupied sites, decreasing the probability $p_k^{(n)}$. For a given initial condition, we integrate, over time, system (6) of ordinary differential equations by using the function ode45 in MATLAB (Mathworks 2011).

We emphasize that our model does not explicitly account for the spatial arrangement of islands. Rather, we describe the colonization process in a spatially implicit way. Because colonization is homogeneous both within islands (governed by a single parameter, c_{in}, for all islands) and between islands (parameter c_{out} for all islands), the spatial structure entirely comprises the distinction between local and long-distance colonization. This leads to a minimal model of the multiscale nature of the colonization process.

We compared our model with the metapopulation model of Levins (1969), which is also spatially implicit but does not consider multiscale colonization dynamics. In appendix B, we construct a mean-field approximation for equations (6), on the basis of the assumption that any island of size n exhibits the mean dynamics of all islands of size n taken together. The resulting dynamics read as follows (see eq. [B7]):

$$\frac{\mathrm{d}f^{(n)}}{\mathrm{d}t} = \left(c_{\mathrm{in}} f^{(n)} + c_{\mathrm{out}} f\right)\left(1 - f^{(n)}\right) - e f^{(n)}, \qquad (7)$$

which are identical to the Levins model when $c_{\mathrm{out}} = 0$. Hence, the approximation predicts that the equilibrium occupancy $f^{(n)^*}$ of an isolated submetapopulation (i.e., when $c_{\mathrm{out}} = 0$) is equal to $f^{(n)^*} = 1 - e/c_{\mathrm{in}}$ if $c_{\mathrm{in}} > e$. However, because of the finite island size, the local submetapopulations ultimately become extinct when $c_{\mathrm{out}} = 0$, even if $c_{\mathrm{in}} > e$ (Ovaskainen 2001; Etienne and Nagelkerke 2002; see also app. C).

The dynamics of a habitat island are affected by the island size in two ways. First, for an isolated island, the larger the island, the longer its (expected) extinction time (app. C). Second, for a connected island, the larger the island, the more colonizers it receives from the rest of the metapopulation. In what follows, we investigate the joint effects that the colonization parameters (c_{in} and c_{out}) and the ISD have on the multiscale metapopulation dynamics.

Results

Slow Extinction Dynamics (Case $c_{out} = 0$*)*

First, we assume that there is no long-distance colonization, that is, $c_{\mathrm{out}} = 0$. Because colonization occurs only within habitat islands, the dynamics of submetapopulations in different islands are mutually independent. In figure 2*A*, we study the effect of island size on the submetapopulation occupancy dynamics. Any (finite) submetapopulation becomes extinct eventually. On small islands extinction occurs relatively quickly (lighter gray), while on larger islands the time to extinction can be very long (darker gray). The extinction time strongly depends on island size n, and the eventual decrease to zero occupancy is exponential in time for any island size n (see app. C). This results in a regular spacing of the curves of figure 2*A* along the abscissa with logarithmic scaling. Additionally, on larger islands the occupancy does not necessarily decrease monotonically to zero. It first tends toward the occupancy level $1 - e/c_{\mathrm{in}}$, which is the equilibrium of equation (7). Large islands can spend a very long time at this occupancy level, a phenomenon known as quasistationarity (Ovaskainen 2001; Etienne and Nagelkerke 2002; see also app. C). The curves in figure 2*A* can also be interpreted as the occupancy dynamics $f(t)$ of a multiscale metapopulation in which all islands have the same size, that is, a metapopulation with homogeneous ISD ($\sigma^2 = 0$).

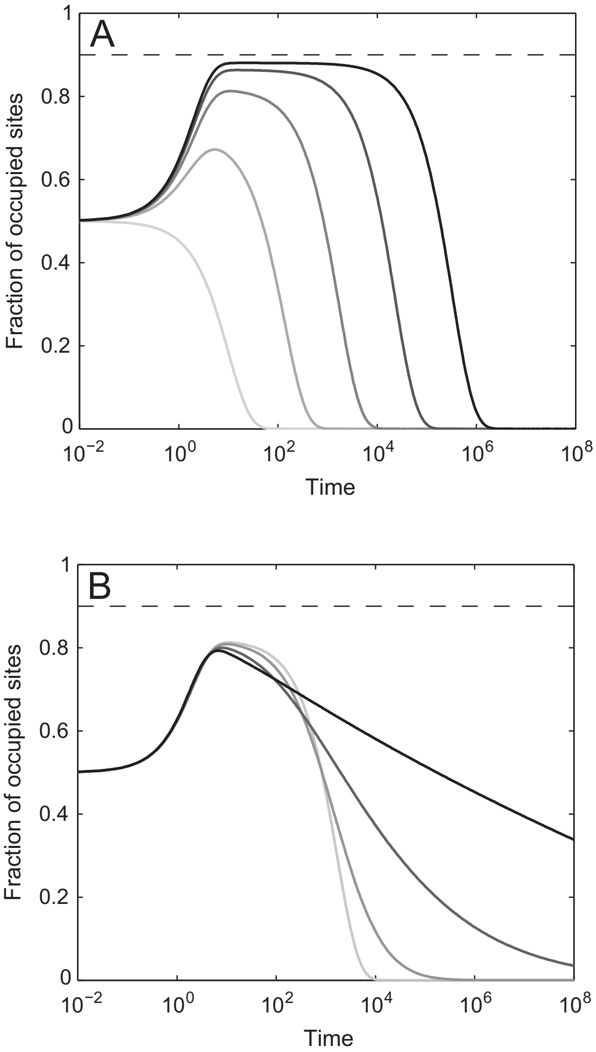

Figure 2: Dynamics of regional occupancy f without colonization between islands ($c_{\mathrm{out}} = 0$). *A*, Homogeneous island size distributions (ISDs; i.e., all islands have the same size). The darker the curve, the larger the island ($n = 1, 3, 5, 7, 9$). *B*, Heterogeneous ISDs with mean island size $\bar{n} = 5$ and different variances σ^2. The darker the curve, the larger the ISD variance. Explicit ISDs are given in appendix A. For both panels, parameter values are $c_{\mathrm{in}} = 1.0$ and $e = 0.1$. The equilibrium occupancy of the corresponding Levins model is given by $1 - e/c_{\mathrm{in}} = 0.9$ (horizontal dashed line). As initial conditions, habitat sites are filled randomly with probability 0.5.

We further study the extinction dynamics for heterogeneous ISDs ($\sigma^2 > 0$) in figure 2*B*. We plot occupancy dynamics for ISDs with the same mean size $\bar{n}$ but with different variances (the darker the curve, the larger the variance). The extinction dynamics are much slower for ISDs with large variance than for the corresponding homogeneous ISD with zero variance (fig. 2*A*). For example, for the ISD with the largest variance, the regional occupancy $f(t)$ is still large after millions of generations.

These slower-than-exponential dynamics can be understood as follows. Recall that the dynamics for different islands are mutually independent (because $c_{\text{out}} = 0$). Hence, for a heterogeneous ISD, the extinction of submetapopulations occurs first on the smallest islands, then on islands of intermediate size, and finally on the largest islands. Even though large islands might be rare, these islands determine the occupancy dynamics once the submetapopulations in smaller islands have become extinct. In particular, as the variance of the ISD increases, the fraction of large islands increases, and the rate of occupancy decrease becomes increasingly slow. For ISDs with large variance, this decrease is much slower than an exponential decrease, despite the exponential extinction dynamics of individual submetapopulations in islands of a specific size n.

Note that, as for homogeneous ISDs, the occupancy dynamics for heterogeneous ISDs do not always decrease monotonically. Specifically, if the initial occupancy within islands is smaller than $1 - e/c_{\text{in}}$, then the time course of the occupancy $f(t)$ reaches a maximum before eventually decreasing. This phenomenon results from larger islands, where occupancy increases to the quasistationary level $1 - e/c_{\text{in}}$ before the eventual extinction dynamics sets in.

It is well known that slow dynamics to extinction are observed in metapopulations close to the critical extinction threshold (Hanski et al. 1996; Bulman et al. 2007). When $c_{\text{out}} = 0$, the extinction threshold is given by $c_{\text{in}} = e$. An infinitely large submetapopulation persists for $c_{\text{in}} > e$ and becomes extinct for $c_{\text{in}} < e$. Are the slow dynamics that we observe in the multiscale metapopulation (fig. 2*B*) an instance of critical slowing down? If this were the case, the dynamics should become increasingly slow when approaching the extinction threshold $c_{\text{in}} = e$. In figure 3, we demonstrate that here we find the contrary. When decreasing c_{in} toward the threshold value $c_{\text{in}} = e$, the slow extinction dynamics vanish. In particular, occupancy $f(t)$ decreases exponentially at the extinction threshold (fig. 3, right panel). We conclude that the observed slow dynamics are unrelated to a slowing down phenomenon occurring close to the critical extinction threshold. Instead, the dynamics become increasingly slow when moving away from the extinction threshold (increasingly large values of c_{in}; extinction threshold is given by $c_{\text{in}} = e$).

Long-Distance Rescue (Case $c_{out} > 0$)

We add long-distance colonization ($c_{\text{out}} > 0$) to the multiscale metapopulation dynamics. In this case, the islands are connected, and their dynamics are no longer independent. When c_{out} is large enough, we expect that large islands surviving longer become sources of colonizers and sustain persistence in the smaller islands that would become extinct otherwise. ISD heterogeneity is expected to influence the relative importance of large islands and thereby to influence this behavior. We show in figure 4 how regional occupancy dynamics vary according to different values of c_{out} when the ISD is homogeneous with $n = 3$ (fig. 4*A*) and when the ISD is heterogeneous with $\bar{n} = 3$ (fig. 4*B*).

The regional metapopulation persists for much smaller values of c_{out} in the case of a heterogeneous ISD than in the

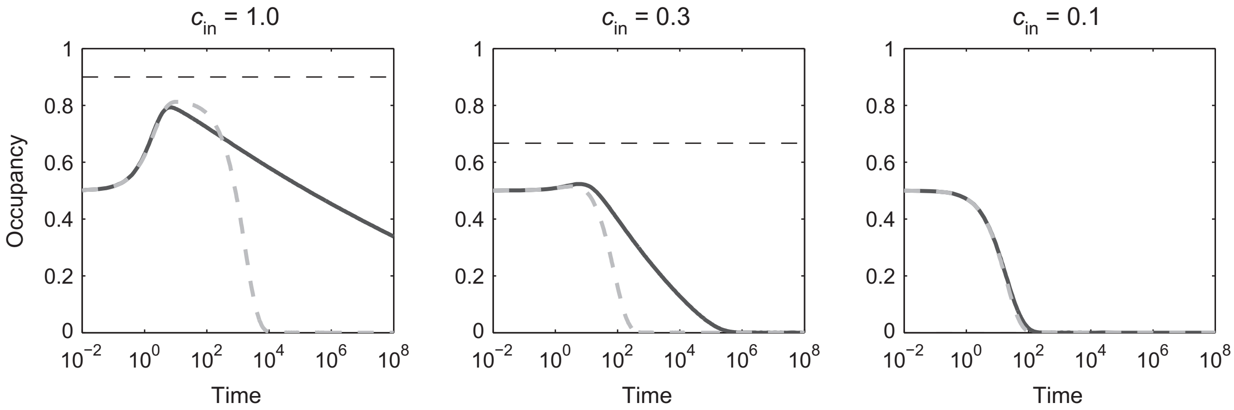

Figure 3: Slow dynamics occur far from the critical extinction threshold. We compare the dynamics of regional occupancy f for different values of within-island colonization c_{in}. Other parameter values are fixed to $e = 0.1$ and $c_{\text{out}} = 0$. The equilibrium occupancy of the corresponding Levins model is nonzero in the left and middle panels (black horizontal dashed line), while the right panel corresponds to the submetapopulation extinction threshold $c_{\text{in}} = e$. Gray dashed line: homogeneous island size distribution (ISD) with island size $n = 5$; black solid line: heterogeneous ISD with mean island size $\bar{n} = 5$ and nonzero variance σ^2 (see app. A for the explicit distribution). For the latter ISD, the occupancy dynamics are extremely slow compared with those of the homogeneous ISD (left and middle panels), but these slow dynamics disappear at the submetapopulation extinction threshold (right panel).

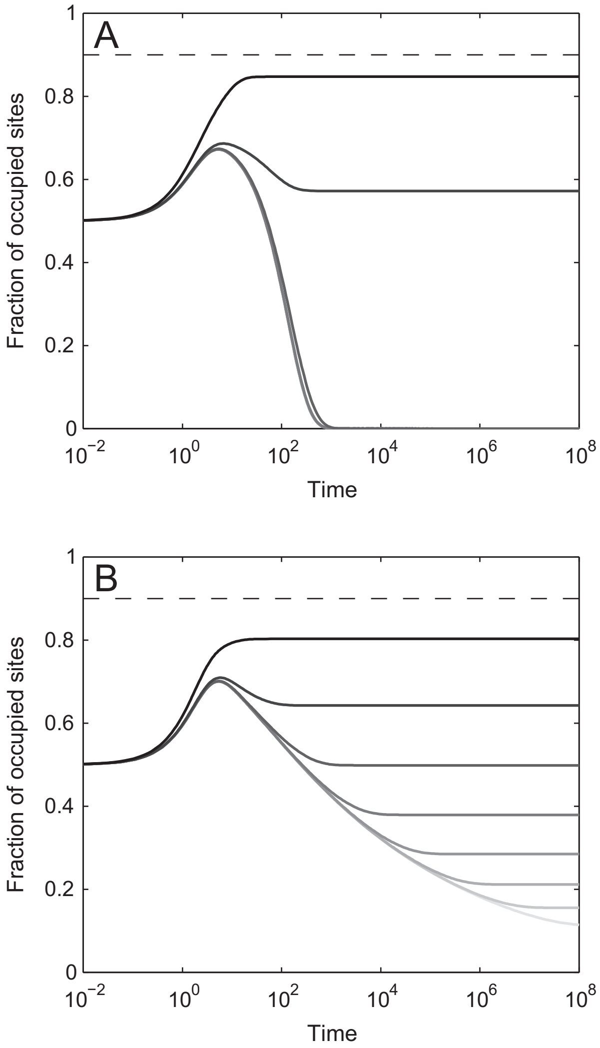

Figure 4: Dynamics of regional occupancy f with colonization between islands ($c_{\text{out}} > 0$). The darker the curve, the larger the between-island colonization ($c_{\text{out}} = 10^{-8}, 10^{-7}, \ldots, 10^{-2}, 10^{-1}$). *A*, Homogeneous island size distribution (ISD) with island size $n = 3$. The curves for $c_{\text{out}} = 10^{-8}, \ldots, 10^{-4}$ coincide. Only the two largest c_{out}'s have nonnull equilibrium occupancy. *B*, Heterogeneous ISD with mean island size $\bar{n} = 3$ and nonzero variance σ^2 (see app. A for the explicit distribution). All curves, even those for the smallest c_{out}'s, tend toward a nonnull equilibrium occupancy.

case of a homogeneous ISD. Because the two ISDs have the same mean island size, this effect is due to the heterogeneity as such. Hence, we find that a heterogeneous ISD enhances regional survival compared with the corresponding homogeneous ISD. This result indicates that long-distance colonization is most effective in metapopulations with islands of varying size. In this case, larger occupied islands act as sources for smaller islands that are liable to become extinct over a short term when isolated. Because the regional connection between islands reduces the extinction risk of local submetapopulations, we call this phenomenon the "rescue effect," by analogy to the rescue effect limiting the extinction probability of populations in a classical single-scale metapopulation (Gotelli 1991).

In appendix D, we analyze the regional metapopulation occupancy at equilibrium. We show that for a fixed value of c_{in}, there is a critical value $c_{\text{out}}^{\text{crit}}$ such that the metapopulation does not persist when $c_{\text{out}} < c_{\text{out}}^{\text{crit}}$ but does persist when $c_{\text{out}} > c_{\text{out}}^{\text{crit}}$. This results quantifies, for fixed parameters of local submetapopulation dynamics, the concept of regional rescue as the minimal input of external colonizers necessary for persistent regional occupancy. Note that, strictly speaking, this persistence is possible only if the number of islands is infinite (as assumed here). However, we expect long-term persistence in the case of a finite but large number of islands as well.

Figure 5 shows the variation of regional equilibrium occupancy f^* according to within-island colonization c_{in} and long-distance colonization c_{out}, and it thus represents a varying regional rescue. For large values of c_{in} (in comparison to extinction rate $e = 0.1$), weak long-distance colonization suffices to maintain an appreciable metapopulation size. This observation depends on the heterogeneity of the ISD. For small values of c_{in} (comparable to an extinction rate $e = 0.1$), even strong long-distance colonization cannot prevent the metapopulation from becoming extinct.

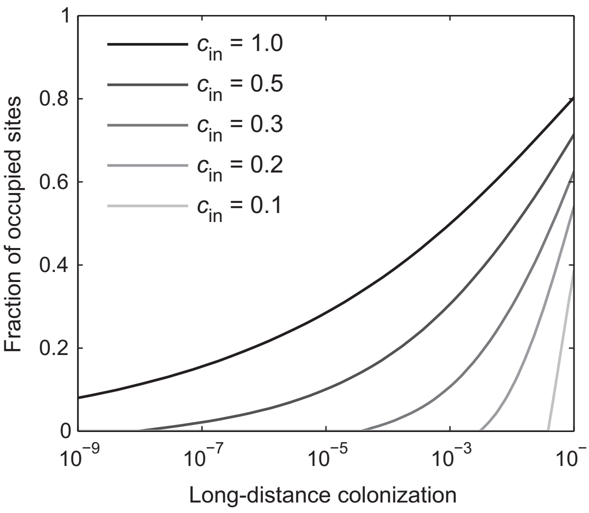

Figure 5: Equilibrium regional occupancy f^* as a function of model parameters. We plot f^* as a function of long-distance colonization c_{out} for different values of within-island colonization c_{in} (gray color scale) and for fixed extinction rate $e = 0.1$. For each curve, there is a critical value $c_{\text{out}}^{\text{crit}}$ such that $f^* = 0$ for $c_{\text{out}} < c_{\text{out}}^{\text{crit}}$ and $f^* > 0$ for $c_{\text{out}} > c_{\text{out}}^{\text{crit}}$ (see app. D). The critical value $c_{\text{out}}^{\text{crit}} = 9.8\ 10^{-15}$ for $c_{\text{in}} = 1.0$ falls outside the range of the *X*-axis. We consider here an island size distribution with mean island size $\bar{n} = 3$ and nonzero variance σ^2 (see app. A for the explicit distribution).

The latter observation is true for both homogeneous and heterogeneous ISDs.

Finally, note that to study the dependencies of the equilibrium occupancy f^*, we can keep the extinction rate e constant. Indeed, a proportional increase in c_{in}, e, and c_{out} does not change the equilibrium occupancy f^*. Such an increase does affect the transitory dynamics, as they become faster with the same constant of proportionality.

Discussion

In this article, we propose an original metapopulation model based on a multiscale habitat structure: local populations occupy habitat sites, which belong to habitat islands of varying size, and the set of habitat islands constitutes the habitat on the regional scale. Habitat sites within islands are connected by local colonization (parameterized by c_{in}), while habitat islands are connected by long-distance colonization (parameterized by c_{out}). Therefore, the model allows us to address how the colonization-extinction process affects species persistence in a multiscale fragmented habitat.

Our model displays three basic types of regional occupancy dynamics: (i) rapid dynamics to extinction, (ii) slow dynamics to extinction, and (iii) (quasi)stationary persistence. Which of these dynamics are realized depends on the relative importance of within- and between-island colonization and on island size variation in the ISD (figs. 2–5). Even rare colonization between islands can yield stationary regional persistence (fig. 5; app. D).

These results provide novel insights of two kinds. First, we show that a realistic heterogeneity of island sizes can drive slow dynamics to extinction of the regional metapopulation, irrespective of any critical phenomenon (fig. 3). This behavior is therefore not related to the slow dynamics usually associated with a critical transition (Hanski et al. 1996; Bulman et al. 2007). Second, we show that long-distance colonization promotes large-scale rescue, enhancing both local and regional persistence. Our results underline the relevance of multiscale metapopulation models for predicting species dynamics in fragmented habitats, especially for conservation purposes.

How ISD Constrains Metapopulation Dynamics and Persistence

Why and how species survive and become extinct in a heterogeneous environment is a central issue in ecology. Identifying the causes of extinction is therefore the aim of a lot of studies and requires the consideration of the life, death, and dispersal of species on several scales, from population demography to metapopulation dynamics and whole-species distributions. Heterogeneity in habitat fragment sizes is known to be crucial for metapopulation persistence, but most metapopulation models consider fragments that include a single population (Hanski and Ovaskainen 2000; Ovaskainen 2002).

Here, we extend the characterization of habitat heterogeneity to account for the size distribution of habitat islands (ISD), themselves including submetapopulations. The present work highlights the key influence of such habitat heterogeneity on regional metapopulation dynamics. We have underlined that the extinction dynamics of submetapopulations within isolated islands depend on island size and determine the regional occupancy dynamics via the ISD (fig. 2). In the absence of long-distance colonization, quasistationary persistence on the regional scale is possible only if large islands can sustain submetapopulations over the long term (large $\bar{n}$ in fig. 2*A*), while rapid extinction occurs when the ISD is dominated by small islands (small $\bar{n}$ in fig. 2*A*). As an intermediate scenario, slow dynamics toward extinction can occur, caused by the sequential extinction of submetapopulations from small to large islands. The latter scenario is expected for ISDs with large variance (fig. 2*B*), which are typical for landscapes with power-law or fractal habitat structure (Bolliger et al. 2003; Kéfi et al. 2007).

Noncritical Slow Dynamics

In the context of global changes, much emphasis has been put recently on understanding and predicting abrupt changes leading to large-scale species extinctions and ecosystem collapse (Zillio et al. 2008; Hirota et al. 2011). Long-distance and long-time correlations are expected at the vicinity of critical transitions, such as the transition to extinction in a metapopulation (Bascompte and Solé 1996; Hanski et al. 1996; Bulman et al. 2007) or the transition to desert in semiarid vegetation (Kéfi et al. 2007). Although a metapopulation is doomed to extinction when crossing the critical threshold, the dynamics can become very slow close to the threshold. The metapopulation can persist for a long time, which generates a so-called extinction debt (Tilman et al. 1994; Hanski and Ovaskainen 2002; Bulman et al. 2007). Critical slowing down is a broader concept representing slow dynamics during ecosystem collapse (Dakos et al. 2011). Early warnings of incipient critical transitions can then be sought in spatial and temporal correlation patterns (Dakos et al. 2008; Scheffer et al. 2009). Recently, however, the validity of interpreting long-range correlation patterns in space and time as early warnings of critical transitions has been challenged because other noncritical phenomena can lead to slow dynamics and long-range correlations (Kéfi et al. 2013).

Our multiscale metapopulation model yields another realistic case of slow dynamics unrelated to a critical transition. In this case, we have found that the slow-dynamics phenomenon is even more pronounced when moving away from the critical threshold (fig. 3). Thus, we stress that extinction debt is not proper to critical transitions of metapopulation collapse. In fact, the noncritical slow dynamics we have described are instances of a well-studied phenomenon in physics called Griffiths phase (Griffiths 1969). This phenomenon occurs when the dynamics of a heterogeneous system are dominated by regions of large size. Although these regions are typically rare, they have very long lifetimes, such that they can determine the overall system properties. Griffiths phases were first discovered in disordered magnetic systems far from their critical point (Griffiths 1969) and have been found in many other systems since then (Bray 1987; Vazquez et al. 2011; Ódor 2013).

Our multiscale metapopulation model also exhibits large regions with long lifetimes (i.e., large islands). The typical time to extinction for an isolated island increases exponentially with island size when $c_{\mathrm{in}} > e$, increasing further when moving away from the critical threshold $c_{\mathrm{in}} = e$ (fig. C1; figs. A1, C1–C3, D1 are available online). Hence, for $c_{\mathrm{in}} > e$ and for a heterogeneous ISD, islands of different size have very different extinction times. The superposition of these extinction times leads to slow extinction dynamics (see fig. 3, left and middle panels). However, at the extinction threshold $c_{\mathrm{in}} = e$, the island lifetime is short and hardly depends on island size (fig. C1). In this case, the extinction dynamics are identical to those for a homogeneous ISD where all islands have the same size (see fig. 3, right panel). This behavior is consistent with the Griffiths phase phenomenon.

Relative Influence of Short- and Long-Distance Colonization

In addition, we have shown that the two components of the colonization process, within and between islands, are important drivers of metapopulation dynamics. Even rare colonization between islands (small c_{out}) suffices to overcome extinction in small islands and to make the system switch from decline to extinction to stationary persistence (figs. 4, 5). Between-island colonization prevents submetapopulation extinction in islands in a manner analogous to the rescue of local populations from extinction due to external colonization (Gotelli 1991). There is a critical value of c_{out} such that stationary persistence is possible if $c_{\mathrm{out}} > c_{\mathrm{out}}^{\mathrm{crit}}$, while deterministic regional extinction is expected otherwise (app. D). Strictly speaking, this result is valid only for an infinite number of islands. For a finite island network, the metapopulation eventually becomes extinct no matter the value of c_{out}. However, if $c_{\mathrm{out}} > c_{\mathrm{out}}^{\mathrm{crit}}$ for a sufficiently large network, regional extinction will occur only after a very long time. Hence, we still expect regional rescue to occur at ecologically meaningful timescales.

In contrast, short-distance colonization (parameterized by c_{in}) determines the (quasi)stationary occupancy within islands and counterbalances local population extinction. The distinct roles played by the two colonization components highlight the importance of addressing the effects of habitat fragmentation on metapopulation dynamics on several spatial and temporal scales. It highlights perspectives to address the evolutionary dynamics of ecological strategies related to persistence and movement on local, island, and regional scales. It could, for instance, provide a novel multiscale framework to address the evolution of dispersal strategies in metapopulations (Olivieri et al. 1995).

An important assumption of the metapopulation approach is that local populations at habitat sites instantly reach their demographic equilibrium, so that the colonization-extinction dynamics solely depend on the extinction rate e and the colonization parameters c_{in} and c_{out}. A much-debated limitation of this assumption concerns the extent to which local populations can be considered independent. If habitat islands consists of continuous habitats, the way to distinguish truly independent populations can be difficult if not impossible (Freckleton and Watkinson 2002; Baguette 2004). In fact, habitat islands can be "megapatches" containing subpopulations instead of independent populations (Cavanaugh et al. 2014). On the other hand, many organisms occupying large patches of continuous habitats show limited dispersal and truly isolated populations, so that the issue pertains to defining large-enough habitat units within habitat islands to meet our assumption.

Although our approach addresses the multiscale nature of habitat fragmentation and the colonization process, it is still in essence a spatially implicit approximation of the colonization process within and between islands. Spatially explicit models will be needed to address in more detail the effects of habitat isolation and overall network connectivity on metapopulation dynamics. Likewise, on the regional scale, although the distribution of island sizes is of central importance to our model, this distribution is implicitly modeled. A more realistic representation could be introduced either by explicitly taking into account island locations (as in lattice models) or, more simply, by varying between-island colonization intensity (as in network models). An exciting perspective would be to enlarge the scope of the spatially realistic model of Hanski and Ovaskainen (2002) and to consider a multiscale habitat network in which nodes are strongly connected within groups (sites belonging to the same island) and weakly connected between groups (sites belonging to different islands; Newman 2006). This would allow us to relate our approach to other recent studies that have highlighted the critical influence of network modularity on metapopulation dynamics (Andrello et al. 2013).

Conclusion and Perspectives

Land-use management strategies can affect the size distribution of habitat islands (corresponding to changes in the

ISD model; see app. A) and the connectivity between islands (corresponding to changes in parameter c_{out}). Such changes can generate rapid or slow dynamics to extinction and biodiversity loss on the regional scale. On the basis of the characterization of habitat ISD and the assessment of habitat connectivity (Mimet et al. 2013), our model allows for predicting species dynamics and persistence. Therefore, our multiscale framework can help design conservation strategies and improve viability analyzes (Drechsler and Johst 2010). Our emphasis on the role played by ISD in species conservation echoes the classical SLOSS (single large or several small) debate but goes beyond this context by addressing dynamical properties related to nested between- and within-island colonization dynamics. The SLOSS framework should therefore be adapted to account for the ISD and the role played by long-distance colonization. Particular strategies could consist of (i) enlarging island sizes or increasing the number of sites within islands when small islands dominate the ISD; (ii) enhancing connectivity between islands to reach the minimal long-distance colonization rate, enabling stationary regional persistence; and (iii) improving local survival within islands when larger islands dominate the ISD. We conclude that appropriate strategies controlling ISD and the two components of the colonization process should help prevent metapopulation extinction and maintain regional biodiversity. Furthermore, our spatially implicit model allows for addressing the role played by habitat heterogeneity in species survival on the intermediate scale of habitat islands. It thereby enlarges the scope of classical metapopulation models, considering the variation of population size as the primary effect of habitat heterogeneity (Hanski and Ovaskainen 2002; Ovaskainen 2002).

The need to bridge the gap between processes driving species dynamics on local and regional scales calls for multiscale perspectives in ecology (Levin 1992). Data on species distributions are more and more intensive and of a large scale—for example, based on naturalistic surveys and citizen science—and metapopulation models must be adapted to investigate the processes underlying these patterns over a broad spatial hierarchy. We therefore think that the multiscale metapopulation model proposed here can be relevant and useful for analyzing such data and forecasting species dynamics. Irrespective of anticipated refinements, our simple model embraces important multiscale properties of metapopulation dynamics, which opens new theoretical perspectives but also has implications for biodiversity management.

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