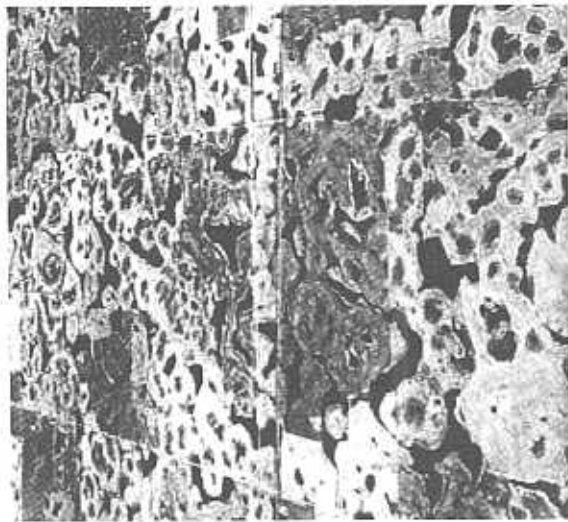


# *Understanding invasions in patchy habitats through metapopulation theory*

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## INTRODUCTION

Many invasive species experience a world that is heterogeneous and patchy, and experience it at multiple scales. In this chapter we will show how metapopulation theory can be used to explore general mechanisms which determine the initial spread and long term establishment of invasive species in novel environments. Metapopulation ecology is a branch of ecology that is focused on how species persist in fragmented or 'subdivided' habitats (Hanski 1999, Hanski and Gaggiotti 2004). Although real landscapes are often highly complex, with admixtures of smooth gradients, fractal edges, and juxtaposed habitats varying in quality, for many species it is natural to construe their world as consisting of sets of suitable habitat patches, arrayed within a largely inhospitable matrix separating those patches. Some such species inhabit naturally patchy habitats, such as islands or ponds (Fig. 1). Some metapopulations appear in artificially constructed habitat networks, such as the remaining fragments of a rain forest surrounded by cattle pastures, or concrete reefs in marine systems. Patch networks can also be formed in more subtle ways, but still make functional metapopulations. The patchy distribution of a host species for a specialist herbivore, parasite, parasitoid, or

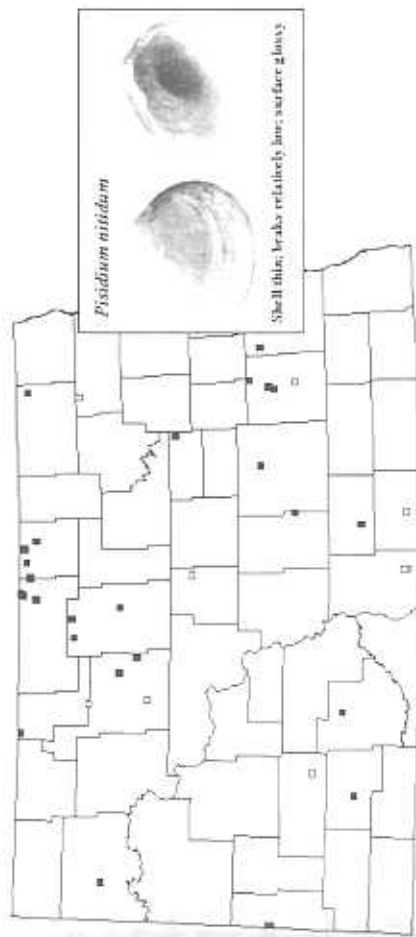


**Fig. 1** Patchy world, ponds in the Northern Prairie farmland. Photo: Stewart, R.E. *et al.* (1971). From Northern Prairie Wildlife Research Center.

commensal (or indeed any vital and spatially delimited resource) can lead to metapopulation dynamics for the specialist. Biological nonlinearities can transform smooth environmental gradients into patchy distributions. For instance, strong Allee effects (positive density dependence at low numbers) can amplify patchiness in the environment. When dispersal is limited, permanent range limits can arise in patchy environments even without overall environmental gradients in the landscape (Keitt *et al.* 2001). Even without Allee effects, if the density of suitable patches declines along an environmental gradient, a species range limit may emerge, when there is no decline in the quality of suitable habitat patches (Holt and Keitt 2000).

A metapopulation is defined as a set of populations connected by dispersal. Dispersal becomes particularly vital to understanding regional population persistence when local populations can become extinct, and must be re-established via colonization. Classical metapopulation theory thus focuses on systems where there is a potential for recurrent extinction. In all metapopulations, long-term species persistence relies on the balance between the rate of extinction of local populations and the rate of new colonizations of empty habitat patches (Fig. 2).

Metapopulation theory is well suited for describing invasions and the establishment of new species into patchy habitats. There are three basic questions



**Fig. 2** Blue squares indicate ponds occupied by *Pisidium nitidum* in the year of sampling. White squares are ponds where *P. nitidum* has gone extinct. Stewart and Kantrud (1971). From Northern Prairie Wildlife Research Center

one can ask about an invasion. First, can an invasion occur at all? Second, given that an invasion occurs, how rapidly does it occur? Finally, following invasion, what impacts does the invader have upon the prior resident community? Metapopulation theory can be used to address each of these basic issues.

We introduce a simple model structure that can be used to summarise and classify some different types of metapopulation invasion scenarios. We examine some special cases, starting with a case in which the invasive species does not compete with any other ecologically similar species. The dynamics of the invasion in this case is then governed by the biology of the invader only, and classic single species metapopulation theory applies. We then consider a general metapopulation model in which the invading species interacts with a native species. We define criteria for when initial invasion occurs and for when long-term coexistence is possible. We also look at some interactions that are specific cases of this general model: a) the invader completely excludes the native species, b) the invader is dependent on the presence of a native species, and, c) there is an intermediate level of competition. We also touch on how spatial heterogeneity can influence invasion. Our overview highlights some general insights about the population biology of invasion which emerge from metapopulation theory.

### NO COMPETITION WITH NATIVE SPECIES — CLASSIC METAPOPULATION BIOLOGY APPLIES

#### Levins metapopulation

Some invasions occur without any obvious competition from native species. For instance, when the marsh-loving muskrat was introduced into central Europe, its numbers grew exponentially (Skellam 1951). In that environment, there were no other obvious aquatic mammals which could interfere with the initial establishment and subsequent growth of this species. In these cases single species metapopulation theory can be applied to investigate basic properties of the invasion (e.g., for the muskrat, its required habitat typically occurs in discrete patches — marshes — separated by a relatively hostile matrix of terrestrial habitats). Moreover, if resident species are relatively fixed in abundance (e.g., the invader initially has little impact), then the residents can be viewed as fixed habitat factors, either hampering or assisting invasion by the focal species. We shall distinguish between two important stages in the invasion process: a, the initial phase of potential successful invasion, or failure, when the invader occurs in relatively few patches, and b, the long term establishment of an invasive species.

First, let us define the model framework. A simple model that captures much of the special metapopulation level effects can be built on the foundation of Richard Levins' (1969) seminal paper on metapopulation theory. He regarded the environment as composed of  $T$  patches of equal quality (where  $T$  is large). He modelled the dynamics of a particular species within this landscape, assuming that each patch is either occupied by members of the species, or empty. Occupied patches send out migrants that settle on patches at random. Each occupied patch sends out migrants that are successful in finding another patch at rate  $m$ . We assume for the moment that we can ignore the spatial arrangement of patches, and that the dispersers from all occupied patches merge into a regional migrant pool. From this pool, they settle uniformly across all patches, both occupied, and empty. If there are  $N$  occupied patches, the total pool size is  $mN$ , and so the rate of arrival of immigrants on each empty (or occupied) patch is simply  $\alpha = mN/T$ . Since there are  $T - N$  empty patches the rate of colonization of new patches is  $K\alpha(T - N)$ , where  $K$  is the probability that a single empty patch is colonized (i.e. converted from empty to occupied by a resident population of the species) by an immigrant. Note that if  $K < 1$ , this means that some colonizations fail. Levins also assumed that each occupied patch becomes extinct (that is changes from occupied to empty) at constant rate  $e$ . These simple assumptions can later be generalized, but are very useful as a first step for developing an intuitive feeling for metapopulation dynamics (Fig. 3). With these assumptions the rate of change in the number of occupied patches is

$$\frac{dN}{dt} = K\alpha(T - N) - eN. \quad (1)$$

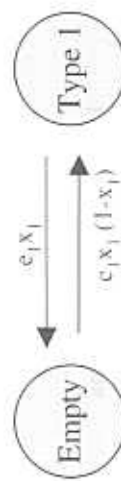


Fig. 3 The classic Levins (1969) metapopulation model for a single species. A given patch can be in one of two states, empty or occupied (by species 1). The rate of change is given by the colonization and extinction rates and the proportion  $x_1$  of occupied patches. ( $c_1$  corresponds to  $K\alpha$  in eqns. 2 and 3).

Let  $x = N/T$  be the proportion of patches that are occupied. Then the above equation can be rewritten in terms of  $x$  as

$$\frac{dx}{dt} = K\alpha(1 - x) - e x, \quad (2)$$

where

$$\alpha = mN. \quad (3)$$

It can be seen from these equations that there is an equilibrium (where the rates of extinction and colonization are equal) at which a certain proportion  $x^* = 1 - e/K\alpha$  of patches are occupied (Levins 1969). The equilibrium is stable since the fraction of occupied patches will always tend towards this equilibrium. (To see that the equilibrium is stable note that if we write equation (2) as  $dx/dt = f(x)$  then  $f'(x^*) < 0$ .)

Even this very simple model can be used to illuminate the conditions causing successful versus failed invasions. To see how an invader will do when it is introduced to an empty patch network, we focus on very low  $x$  values (this is usually a reasonable assumption regarding the initial conditions of natural or inadvertent invasions, but it may not always be appropriate for deliberate, large-scale introductions). From equations (2) and (3)

$$\frac{1}{x} \frac{dx}{dt} = Km - e \text{ for small } x. \quad (4)$$

Thus the species can invade if  $Km > e$ . If invasion is possible the invading species will increase its presence until the equilibrium size  $x^*$  is reached. (see Box 1 for a list of model parameters.)

**Box 1****Levins model definitions**

$T$  = the number of habitat patches available  
 $N$  = the number of habitat patches occupied by the study species  
 $m$  = rate of migration from an occupied patch  
 $\alpha$  = the rate of arrival of immigrants to each of the  $T$  patches  
 $K$  = the probability that a single empty patch is colonized (i.e., converted from empty to occupied by a resident population) by a single immigrant  
 $e$  = rate at which an occupied patch goes extinct  
 (Overall) rate of colonization =  $K\alpha(T - N)$   
 (Overall) rate of extinction =  $eN$   
 $x^*$  = equilibrium patch occupancy (where rate of colonization and rate of extinction are equal)

**Habitat loss model**

$U$  = the number of unsuitable patches  
 $h$  = fraction of the landscape that is habitable for the study species

**Generalized model**

$E(\alpha)$  = single patch extinction rate as a function of immigration  
 $C(\alpha)$  = single patch colonization rate as a function of immigration  
*Rescue effect* = immigration into a patch lowers patch extinction risk  
*Anti-rescue effect* = immigration into a patch increases patch extinction risk  
*Allee effect* = colonization success is a non-linear function of immigration, accelerating with increasing immigration rate  
*Anti-Allee effect* = non-linear colonization success, decelerating with increasing immigration rate

**Model with two distinct habitats**

$h_i$  = the fraction of a landscape that is covered by type  $i$  habitat patches  
 $p_i$  = the fraction of the landscape that is both of habitat type  $i$  and occupied  
 $e_i$  = extinction rate of type  $i$  patches  
 $c_i$  = colonization onto empty patches of type  $i$ , due to migrants generated by occupied patches of type  $j$   
 $\lambda_i$  = rate of increase in patch occupancy of species when it is rare, and only patch type  $i$  is present.

**Box 1****Two species metapopulation model**

$N_1$  = the number of patches occupied by species 1  
 $N_b$  = the number of patches occupied by both species  
*Patch states* = Empty, Type 1, Type 2, Type B  
 $m_1$  = migration rate of species 1 migrants from a Type 1 patch  
 $\bar{m}_1$  = migration rate of species 1 migrants from a Type B patch  
 $C_1(\alpha_1)$  = colonization rate of an empty patch by species 1 immigrants  
 $\bar{C}_1(\alpha_1)$  = colonization rate of a Type 2 patch by species 1 immigrants  
 $E_1(\alpha_1)$  = extinction rate of a Type 1 patch  
 $\bar{E}_1(\alpha_1)$  = extinction rate of species 1 in a Type B patch

*Biological conclusions from Levins model*

Failed invasions can arise either from processes that affect extinction, or from the details of the process of colonization. There are many reasons extinction rates may be high in a novel environment. If within each patch the intrinsic growth rate ( $r$ ) of the invader is negative (i.e.,  $r < 0$ , so births  $<$  deaths), then extinction is inevitable (unless there is very rapid evolution, see Gomulkiewicz and Holt 1995). This could arise because of unfavorable abiotic conditions, or because superior competitors or effective predators are present. But even if  $r > 0$ , if a patch has a very low local carrying capacity, it may suffer high rates of extinction due to demographic stochasticity: if it has a low  $r$ , it may also not be able to recover rapidly from catastrophes, and so randomly walk to extinction. Environments with frequent catastrophes are likely to generate high extinction rates for invasive species, so all else being equal, are not as likely to be invaded.

But equal weight should be given to constraints on the colonization process as potential causes of failed invasions. In the terms of the basic model, if  $m$  is reduced, so is the likelihood of invasion. The quantity  $m$  combines two things: a per capita rate of emigration from an occupied patch, and the number of individuals present there and available to emigrate. Species that are sedentary, or philopatric, are likely to have a low  $m$ . Such species should tend to be poor invaders. For species with equal per capita rates of emigration, those species with the highest abundance within occupied patches can generate a high abundance of migrants, and



so experience the highest colonization rate into empty patches. Large  $m$  should thus reflect both high fecundity and high survival of emigrants across the matrix habitat separating habitable patches. The probability of successful colonization ( $K$ ) also varies greatly among species. For instance, a high  $K$  can be expected in species where the migrants have high fecundity, so that one or a few immigrants can establish a successful population (by quickly producing a large number of offspring, thereby avoiding initial demographic stochasticity), and when individuals are long-lived. Birth-death process models (e.g. as in MacArthur and Wilson 1967) reveal that in comparing species with a given intrinsic growth rate ( $r$ ), the probability of extinction is lower for species with lower absolute death rates. Conversely, species which are at risk of frequent stochastic mortality events are likely to have low intrinsic colonization propensity, and so have a low  $K$ . Immigrants are likely to be unfamiliar with the details of local resources, refuges, and mortality risks, and if learning new conditions is slow or unreliable, immigrants may be vulnerable to rapid elimination in novel environments.

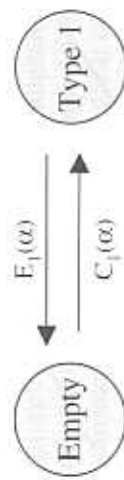
One mathematically slight but biologically significant generalization of the Levins' model suggested by Lande (1987) and Nee and May (1992) is to recognize that in a landscape, not all empty patches are suitable. If we assume that out of  $T$  patches,  $U$  are unsuitable, then  $h = 1 - U/T$  is the fraction of the landscape that is potentially occupiable by the species. Working back through the same steps as before, we end up with  $dx/dt = K\alpha(h-x)ex$ . The invasion criterion now becomes  $Kmh > e$ . As noted for a somewhat different version of the model in Holt and Keitt (2000), this simple formulation of invasion encompasses a great deal of biology. In addition to the mechanisms mentioned in the previous paragraphs, another reason why an invasion could fail is that insufficient suitable habitat is available. Even if each suitable patch could sustain a population on its own over a reasonable time scale, if there are too few of them, colonization may not be able to match even a low rate of extinction. Holt and Keitt (2000) show how these ideas permit one to consider in a unified fashion many different hypotheses that have been put forth regarding the factors causing distributional range limits.

The theoretically best invader would have low extinction risk and high  $m$ . The theoretical 'best' is likely to be unfeasible, because there are biological constraints, such as tradeoffs between life history traits (e.g., reproduction and longevity in animals, and between development of vegetative propagules and seed production in plants).

#### Dynamic Levins type metapopulation

The Levins model clarifies many essential features of metapopulation dynamics, but it rests on quite simple assumptions about how migration influences both colonization and extinction (Hanski 1999). The basic Levins framework has been extended to several specific cases in different studies, including for example a linear rescue effect (Hanski 1982, Gotelli and Kelly 1993), and a specific nonlinear Allee effect (Hanski 1994). The Levins model was recently generalized to allow

for these and other dynamic influences from migration on both colonization and extinction rates (compare Figs 3 and 4) (Harding and McNamara 2002). The generality is obtained by expressing both colonization and extinction rates as functions of immigration rate, as we now describe.



**Fig. 4** An extension of Levins' model (Fig. 3). Here the rate of colonization and extinction are not fixed constants, but can be any function of immigration rate ( $\alpha$ ). This model can therefore capture several types of single species dynamics, such as Allee effects, rescue effects and anti-rescue effects (Harding and McNamara 2002).

It is useful to think of metapopulation processes at two scales. The smallest scale is the patch. The subpopulation inhabiting a patch has a given risk of local extinction  $E(\alpha)$ , that may be influenced by the rate of immigration  $\alpha$  to the patch. Empty patches are colonized at rate  $C(\alpha)$ , that very likely depends on  $\alpha$ . Given these 'local rates of change' the overall rate of change in the proportion ( $x = N/T$ ) of patches that are occupied in the whole metapopulation is

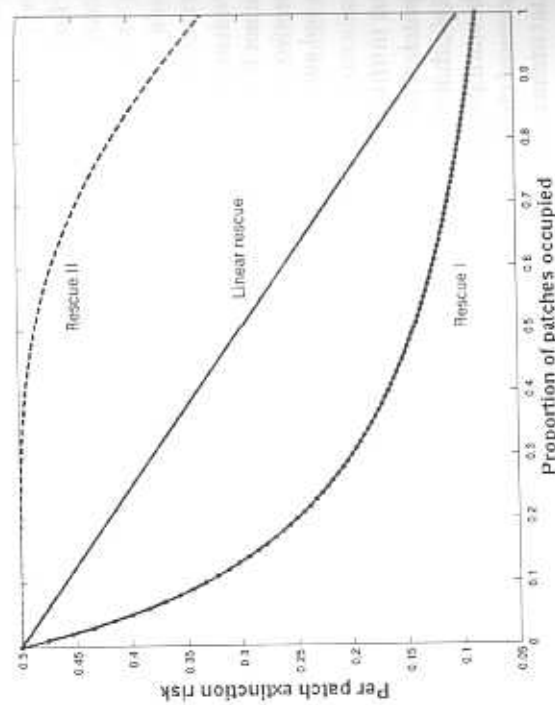
$$\frac{dx}{dt} = C(\alpha)(1-x) - E(\alpha)x \quad (5)$$

(Harding and McNamara 2002). (Here we again assume that all patches are potentially occupiable.) The Levins model is then a special case of this model with extinction function  $E(\alpha) = e$  and colonization function  $C(\alpha) = K\alpha$ . As described below, a variety of biological processes can be mimicked phenomenologically with this extended framework.

#### Dynamic extinction functions

The original Levins extinction function has a constant value,  $e$ , that is independent of immigration rate. In a metapopulation it can be important to allow the extinction rate of a patch to depend on immigration into that patch. Immigrants can for example lower patch extinction risk by providing a demographic contribution to declining populations or by introducing new good genes (e.g., reducing inbreeding depression (Saccetti *et al.* 1998)); this is the rescue effect (Brown and Kodric-Brown 1977, Hanski 1982). Following a catastrophe, immigrants can

speed the recovery of the population, allowing it to more rapidly rebound from dangerously low densities. Depending on the underlying processes leading to a rescue effect, the extinction function can have different shapes (Fig. 5).



**Fig. 5** Illustration of rescue effect functions. The rate of per patch extinction can sometimes decrease as immigration rate increases. Three different types of response to increased immigration are illustrated.

However, in other circumstances immigration can lead to increased extinction risk — we term this pattern an anti-rescue effect. This can for example be due to immigrants carrying parasites or diseases, or because immigrants carry different genes, breaking up locally adapted beneficial gene combinations (Rolán-Alvarez *et al.* 1997). In predator-prey systems, increasing immigration can sometimes destabilize local interactions, making excursions to low densities and hence local extinctions more likely (Schöps 1999, Holt 2002; see review in Hoopes *et al.* 2005). With all these mechanisms, increasing immigration rate over some range of values is likely to boost local extinction rates.

#### Dynamic colonization functions

In Levins' model the colonization rate per patch increases linearly with the immigration rate, and hence increases linearly with the number of occupied patches

However, colonization might take other forms as well. It is common for a species to have problems in initial establishment in a patch when the number of immigrants is low, due to demographic skews (lack of adults or males for example), difficulty in finding mates, or inbreeding. The phenomena of disproportionately low colonization success when the immigration rate is low is an example of an Allee effect (Allee 1931, Hanski 1994).

The opposite, when colonization by a single migrant is more successful when there are few other migrants is termed an **anti-Allee effect** (Harding and McNamara 2002). It can occur if migrants do not settle at random but avoid conspecifics (e.g. territoriality), so that migrants actively seek unoccupied patches. This leads to a very rapid colonization initially, but after a while most patches are occupied and the effect should become less important. It is also conceivable that if resources are exploited which have low rates of renewal, an increase in the number of immigrants could lead to rapid overexploitation, resource depletion, and thus a reduced probability of successful establishment. Both these mechanisms can lead to an anti-Allee effect at the metapopulation level.

Impacts by resident generalist predators upon colonization by an invasive prey species are likely to shift between anti-Allee effects and Allee effects, depending on the quantitative details of the predator's functional response, and the number of immigrants. If a resident predator has a type III (sigmoidal) functional response, then over a range of low prey numbers, an increase in prey density due to an increasing number of migrants leads to an increase in the per capita mortality rate inflicted on the prey (e.g., because the predator becomes increasingly aware of the novel prey with increasing exposure to it, and so is more likely to cause prey extinction with increasing numbers of colonists). This can be viewed as an anti-Allee effect (which could broadly describe any kind of negative density dependence operating at low densities which can negatively affect colonization success), but typically at higher prey densities, most predators have saturating functional responses (e.g., due to limited handling time or gut capacity), so the per capita mortality rate experienced by prey declines with increasing prey density. In this range, an increasing number of migrants may enhance colonization, by diluting the impact of predation. So whether or not a colonising species experiences an Allee, or an anti-Allee effect, due to resident predators will depend upon both the predator's functional response, and the number of migrants.

#### Who is a good invader in the single species system?

To analyse whether a species can invade into a patchy landscape, we suppose that the species has been introduced in a small number of patches. We can then ask whether the number of occupied patches tends to grow or decline. In terms of the generalized metapopulation model described above we are concerned with whether  $dx/dt > 0$  when  $x$  is small. This depends on the behaviour of the colonization and extinction functions for small  $x$ , and hence small  $\alpha$ . Suppose that

$$C(\alpha) \approx K\alpha \text{ for small } \alpha, \quad (6)$$

and

$$E(\alpha) \approx e \text{ for small } \alpha. \quad (7)$$

Thus for small numbers of occupied patches the metapopulation behaves as described by Levins' model with parameters  $K$  and  $e$ , although it may behave very differently when the number of occupied patches increases. With this assumption, approximation (4) is still valid, so that the species can invade if  $Km > e$ .

#### When does an invasive species get established in a single species metapopulation?

Figure 6a-f illustrate the extinction rate (white surface) and colonization rate (black 'hills') for single species metapopulations. It shows how different combinations of  $C(\alpha)$  and  $E(\alpha)$  influence the equilibria (where the two surfaces meet). Depending on the functions  $C(\alpha)$  and  $E(\alpha)$  there may exist: at least one non-trivial equilibria in patch occupancy ( $x^* > 0$ ) such that total colonization and extinction rates balance when a proportion  $x^*$  of patches are occupied. In some cases there may be more than one such equilibrium (i.e., for a given  $m$  the two rates are equal at two or three different  $x$ ; see Fig. 6 b,c,e,f) (Harding and McNamara 2002). The exact shapes of  $C(\alpha)$  and  $E(\alpha)$  are important also for the extinction risk of the entire metapopulation, at low patch numbers (Fig. 7). The occurrence of multiple equilibria has earlier been studied in more complex metapopulation models (Hanski and Gyllenberg 1993, Gyllenberg *et al.* 1997). If at least one equilibrium exists then there is at least one stable equilibrium. Here by 'stable' we mean that if  $x$  is initially close to  $x^*$  then the proportion of occupied patches will tend to  $x^*$  over time. In Levins' model there is a unique equilibrium (that is stable) if  $Km > e$  (Fig. 6 a) and there is no equilibrium if  $Km \leq e$ . Thus in this particular model a stable equilibrium exists if and only if the species can invade!

For other shapes of  $C(\alpha)$  and  $E(\alpha)$  it is also true that if a species can invade, then the proportion of occupied patches will certainly increase and tend to a stable equilibrium. In general, however, the converse need not hold, and the existence of an equilibrium is not equivalent to the ability to invade. To see this, suppose that there is an Allee effect. Thus the patch colonization function  $C(\alpha)$  is an accelerating function of  $\alpha$  for small  $\alpha$ . Let the patch extinction function be as in Levins' model; i.e.,  $E(\alpha) = e$  (a constant). Then for suitable choice of  $e$  the total extinction rate exceeds the total colonization rate for small  $x$ , but colonization exceeds extinction if  $x$  is somewhat larger (Fig. 6c). Thus the species cannot invade; however, if the proportion of patches occupied were artificially increased so as to exceed some critical level, then the proportion would continue to increase and tend to a stable equilibrium.

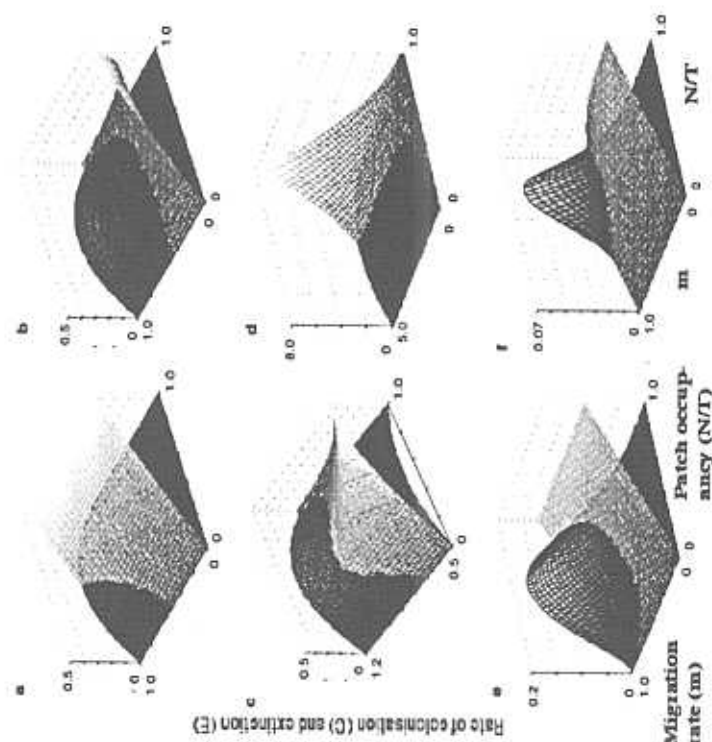


Fig. 6 A range of metapopulations with different dynamics of the model in Fig. 4. White surfaces are total extinction risks and black hills total colonization rates. a. An ordinary Levins metapopulation. b. A rescue effect makes extinction risk decline with higher migration rates. c. A different kind of rescue effect. d. Anti-rescue effect leads to higher extinction risk with higher migration rates. e. The colonization function is bell-shaped; an Allee effect prevails. f. An example with both a rescue and Allee effect.

#### Heterogeneous landscapes

Holt (1997) considered a generalization of the standard Levins' metapopulation model to a landscape with two distinct habitats. A fraction  $h_1$  of the landscape is comprised of patches of type  $i$ . The fraction of habitat patches that are type  $i$  and occupied by the species is denoted by  $p_i$ . Necessarily, we have  $p_i \leq h_i$ , and  $h_1 + h_2 \leq 1$ . (If in the latter case, the inequality holds ( $h_1 + h_2 < 1$ ), some patches in the landscape are unsuitable for occupancy.) Using the standard Levins' notation,  $e_i$  denotes extinction on occupied patches of type  $i$ , and  $c_i$  is colonization onto empty patches of type  $i$ , due to migrants generated by occupied patches of type  $j$ . The equation for dynamics of  $p_i$  is  $dp_i/dt = (c_{1i}p_1 + c_{2i}p_2)(h_i - p_i) - e_i p_i$  (a similar equation describes dynamics in the second habitat type).



The total occupancy by the species in the landscape is  $p = p_1 + p_2$ . If we sum the dynamical equations for change in occupancy, we get an expression for  $dp/dt$ . In general, this does not simplify to a form in just  $p$ . However, if all the colonization rates  $c_i$  are equal to a constant,  $c$ , and both patches have the same extinction rates, the original Levins model emerges. In other words, arbitrary distinctions among habitats can simply be ignored. However, if patch type influences either colonization or extinction, landscape heterogeneity can influence metapopulation dynamics (e.g., patch types differ in  $K$  or  $m$ ).

All the factors mentioned above which influence colonization and extinction rates can potentially show variation among habitat types. For instance, an individual born in a habitat patch of type  $i$  before emigrating might become acclimated to the abiotic conditions in its natal site (e.g., as in physiological adaptation to thermal conditions), and so either preferentially seek out similar habitats when it disperses, or be vulnerable to high mortality if it settles into a different habitat, leading to failed colonization.

If only patch type  $i$  is present, the initial growth rate of the species, when rare, is  $\lambda_1 = c_i h_i - e_i$  (as in the standard Levins model). With both patch types present, the asymptotic growth rate of the invading species turns out to be  $\lambda = (1/2) (\lambda_1 + \lambda_2 + \sqrt{(\lambda_1 - \lambda_2)^2 + 4e_1 e_2})$  (Holt 1997).

Manipulating this expression leads to several simple conclusions. First, a species which is a generalist may be able to invade and persist because it can enjoy cross-habitat colonization, whereas otherwise similar habitat specialists would go extinct (i.e., experience failed invasions). Second, sometimes utilizing a second habitat may be crucial in permitting a species to persist in a landscape, even if there is no colonization among patches of this second type (condition 5 in Holt 1997). This can happen if all colonization from and of the second habitat type is into and from habitats of the first habitat type (e.g., because patches of the second habitat type are widely spaced), but the second habitat type has a lower extinction rate than does the primary habitat type. This can be viewed as a kind of 'spatial storage effect'. It would be interesting in future work to extend this two-habitat model using the generalized approach of Harding and McNamara (2002). Colonization among some habitats may permit rescue effects, even while colonization among others resembles the anti-rescue pattern. In such cases, the expected dynamics of invasion would be quite sensitive to the relative proportions of the landscape occupied by the distinct habitat types.

#### INTERACTIONS WITH A NATIVE SPECIES

An invasive species can interact with a native metapopulation in the same patch network in various ways, with net effects on the likelihood of invasion ranging from positive to negative. For instance, when species compete for the same limiting resource within patches, competitive exclusion is likely. Metapopulation dynamics can nonetheless permit invasion by an inferior species, if it is superior

at colonization of empty patches (Levins and Culver 1971, Tilman 1988). This requires a tradeoff between competition and colonization, allowing the inferior competitor to exploit more effectively the empty habitat patches left by the superior competitor when it suffers extinctions (Amarasekare 2003).

Metapopulation dynamics can also lead to exclusion that would otherwise not occur (Holt 1997). For instance, one species can delimit a second species indirectly, by hosting a pathogen that is more harmful to the second species (Holt and Lawton 1993). An example is the gradual eradication of the native noble cray fish (*Astacus astacus*) in Sweden which is being replaced by the North American signal cray fish (*Pacifastacus lenisculus*), mediated by a shared infectious disease. The invasive species carries a fungus (*Aphanomyces astaci*) to which it itself appears to be immune, whereas the native species is severely impacted by the parasite (Bangyeekhun 2002). In a metapopulation, such indirect exclusion may occur even if the two species occupy distinct habitat patches; in this example, if fungal spores disperse widely the invasive species could provide a landscape 'reservoir' for the pathogen, which can eliminate the native species even in patches where the invasive species itself never occurs.

There can also be facilitative interactions between invasive and resident species. In the literature on succession, there are many examples of early colonizers facilitating invasion by later colonists (e.g., nitrogen-fixers may need to colonize prior to other species) (Connell and Slatyer 1977). In this case, one species alters the abiotic environment so as to enhance colonization or reduce extinction for a second species. Moreover, one species may require another species as a resource. Invasions by specialist predators, parasites or herbivores will almost always depend upon the presence of their required prey or hosts.

#### A flexible model which allows for many kinds of interactions

We will now look at invasions in which each of two species has interlinked metapopulation dynamics, extending a phenomenological metapopulation model of Hanski (1999) and others (Fig. 8) to include different types of colonization and extinction functions, and differential migration rates. We use this model to classify different types of interactions between an invasive species and a native species.

We consider a metapopulation with  $T$  identical patches. Each patch can be in one of four states: Empty, Type 1 when species 1 is present, Type 2 when species 2 is present, or Type B, when both are present (Fig. 9).

#### Migration

Each Type 1 patch sends out (successful) species 1 migrants at rate  $m_1$ . Each Type 2 patch sends out (successful) species 2 migrants at rate  $m_2$ . Each Type B patch sends out (successful) species 1 migrants at rate  $\tilde{m}_1$  and sends out (successful) species 2 migrants at rate  $\tilde{m}_2$ . Note that the difference between  $m_1$  and  $\tilde{m}_1$  measures how much species 2 can suppress or enhance the migration rate of



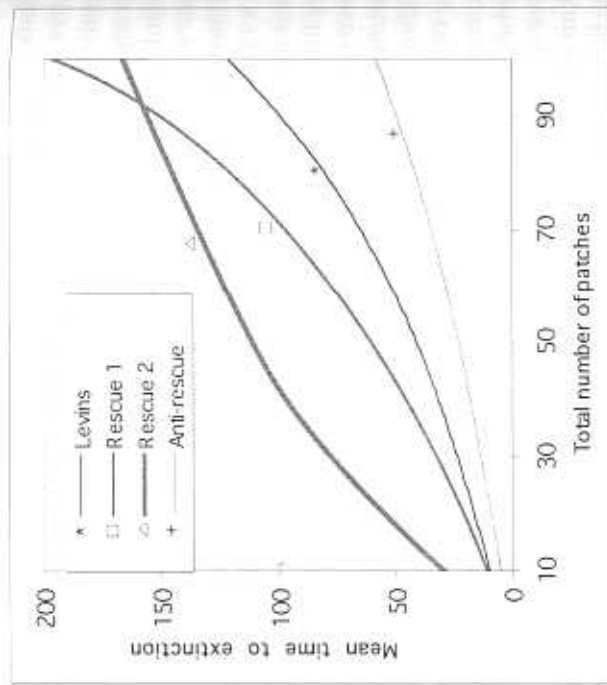


Fig. 7 The risk of extinction at low patch numbers depend on the shape of the C and E functions (see Fig. 6) From Harding and McNamara 2002.

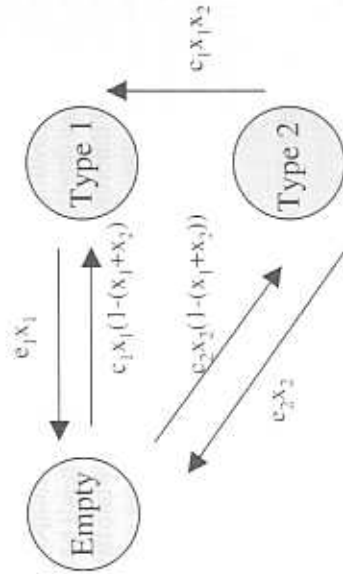


Fig. 8 A metapopulation model for two species. Species 1 is competitively superior and excludes species 2 from patches. Species 2 can persist if it has a higher colonization to extinction ratio than species 1 (Nee and May 1992).

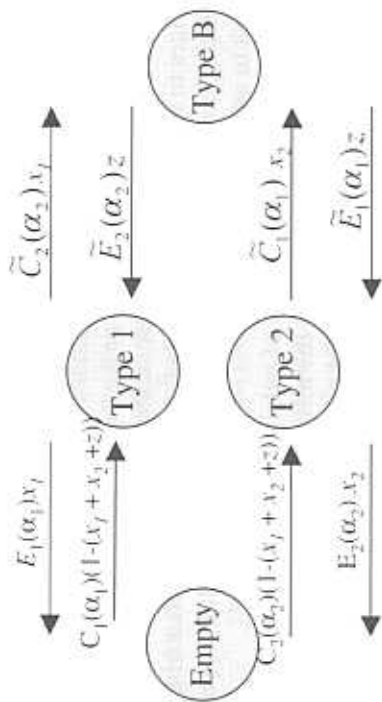


Fig. 9 A metapopulation model specifically designed to study invasive species (eq. 9-12). A patch can be in one of four states: empty, occupied by species 1, or species 2 or occupied by both species (B). This model allows us to explore many sorts of influences that invasive species can have on a native species. The extinction (E) and colonization rates (C) are functions of immigration ( $\alpha$ ).

species 1. Similarly for species 2, the difference in migration parameters reflects interspecific impacts on the rate at which emigrants are emitted from jointly occupied patches. These differences could occur due to changes in density within patches, or due to changes in individual behavior in the face of the other species (e.g., a prey species may spend more time in hiding in the face of a predator, and thus be less likely to emigrate from patches containing both predators and prey).

Initially, we assume that migrants settle at random. Suppose that the number of Type 1 and Type B patches are  $N_1$  and  $N_B$  respectively. Then species 1 migrants arrive at each patch in the environment at rate

$$\alpha_1 = (N_1 m_1 + N_B \bar{m}_1) / T. \tag{8}$$

The rate of arrival of species 2 migrants,  $\alpha_2$ , is similarly defined.

Colonization

Each empty patch is colonized by species 1 migrants (and hence becomes a Type 1 patch) at rate  $C_1(\alpha_1)$ . Empty patches are colonized by species 2 migrants (and become Type 2) at the rate  $C_2(\alpha_2)$ . Each Type 2 patch is colonized by species 1 migrants (and hence becomes a Type B patch) at rate  $\tilde{C}_1(\alpha_1)$ . Similarly each Type 1 patch is colonized by species 2 migrants and is converted to a Type B patch at the rate  $\tilde{C}_2(\alpha_2)$ . Note that we never have an empty patch simultaneously colonized by both species 1 and 2.

### Extinction

A Type 1 patch changes to an empty patch at rate  $E_1(\alpha_1)$ . A Type 2 patch changes to an empty patch at rate  $E_2(\alpha_2)$ . A Type B patch (which has both species) changes to a Type 2 patch when species 1 goes extinct, at rate  $\bar{E}_1(\alpha_1)$ . Similarly a Type B patch changes to a Type 1 patch at rate  $\bar{E}_2(\alpha_2)$ . We assume that in a patch with both species, there are not simultaneous extinctions, taking Type B patches directly back to an empty state.

In this model, the rate of change of patch state depends on migration rates from both the two single species and the mixed species patches. The two species can thus influence each other by altered extinction and colonization rates, both of which can involve altered migration rates. (see Fig. 9.)

### Possible interactions between species

Now consider interactions between the two species (Fig. 9). If species 1 competes with species 2, then species 2 may be adversely affected by the presence of species 1 in various ways. It may be more difficult for species 2 to colonise a patch that is already occupied by species 1 than to colonise an empty patch; i.e.,  $\bar{C}_2(\alpha_2) < C_2(\alpha_2)$ . If species 1 can colonise a patch currently occupied by species 2, so as to produce a patch with both species, then this may increase the probability that species 2 goes extinct on the patch; i.e.,  $\bar{E}_2(\alpha_2) > E_2(\alpha_2)$ . The presence of species 1 may also reduce the rate at which species 2 sends out migrants from the patch; i.e.,  $\bar{m}_2 < m_2$ . This will reduce the immigration rate  $\alpha_2$ , which will tend to reduce the rate at which patches are colonized by species 2.

If  $\bar{m}_2 < m_2$ , there is a possible beneficial effect to species 2 for species 1 to also be present in a patch. Given a strong anti-rescue effect, (i.e., increased immigration increases extinction rate) a reduction in the immigration rate  $\alpha_2$  may reduce the rate at which species 2 dies out on patches. Whether competition from species 1 is beneficial or not may depend on the number of patches already occupied by species 2. For example, if the anti-rescue effect only becomes marked at high immigration rates, competition may be deleterious to species 2 when it is rare but beneficial when it is common. In a sense, given metapopulation dynamics and an anti-rescue effect, a competitor (as measured by a reduction in the size of the migrant pool generated by patches) may dynamically be a mutualist.

If instead of being a competitor, species 2 is a predator that benefits from the presence of prey species 1, we would have  $\bar{C}_2(\alpha_2) > C_2(\alpha_2)$ ,  $\bar{E}_2(\alpha_2) < E_2(\alpha_2)$  and  $\bar{m}_2 > m_2$ . In the extreme case where species 2 is a specialist consumer (e.g. a parasite or parasitoid) that is totally dependent on the presence of species 1;  $C_2(\alpha_2) = 0$ ,  $E_2(\alpha_2) = \infty$  and  $m_2 = 0$ , and the model reduces to a three patch system similar to epidemiological models. The direction of the inequalities for the growth of species 1 depend on the biology of the interaction. In a typical predator-prey interaction, the inequalities are all reversed for species 1.

In some cases, however, as noted by Holt (1997, 2002) a predator may instead reduce the rate of extinction of its prey: for instance the presence of the predator may prevent the prey species from overexploiting its own resource base. Although this is an interesting possibility (e.g., generating alternative landscape states), below we focus instead on more classical predator-prey systems where the predator is harmful for prey persistence in a patch.

### Dynamics of the two species metapopulation

We now analyse the rates at which patch occupancy in the two species metapopulation changes over time. Denote the fraction of patches with species 1 only by  $x_1$ , the fraction with species 2 only by  $x_2$  and the fraction with both species present by  $z$ . The fraction of empty patches is thus  $1 - (x_1 + x_2 + z)$ , and the rates of change of patch occupancy are

$$\frac{dx_1}{dt} = C_1(\alpha_1)(1 - (x_1 + x_2 + z)) - E_1(\alpha_1)x_1 - \bar{C}_2(\alpha_2)x_1 + \bar{E}_2(\alpha_2)z \quad (9)$$

$$\frac{dx_2}{dt} = C_2(\alpha_2)(1 - (x_1 + x_2 + z)) - E_2(\alpha_2)x_2 - \bar{C}_1(\alpha_1)x_2 + \bar{E}_1(\alpha_1)z \quad (10)$$

$$\frac{dz}{dt} = x_1\bar{C}_2(\alpha_2) + x_2\bar{C}_1(\alpha_1) - z(\bar{E}_1(\alpha_1) + \bar{E}_2(\alpha_2)) \quad (11)$$

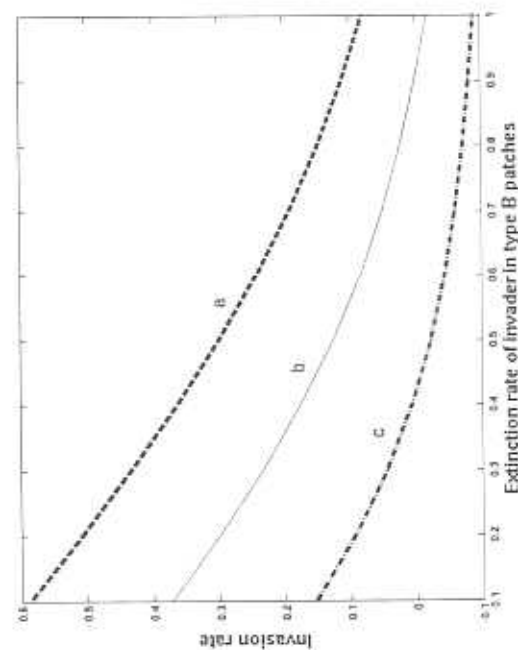
Here the immigration rates can be expressed in terms of  $x_1$ ,  $x_2$  and  $z$  as

$$\alpha_1 = x_1m_1 + z\bar{m}_1 \quad \text{and} \quad \alpha_2 = x_2m_2 + z\bar{m}_2 \quad (12)$$

### Criteria for invasion

#### Initial invasion

We now describe the criteria for the initial phase of an invasion. We assume that the native species (species 1) currently occupies a proportion  $x_1$  of all patches, where this proportion is a stable equilibrium for the metapopulation with just species 1 present. We then introduce the invader (species 2) into a few patches, and ask whether the frequency of occurrence of the rare invading species increases or declines. Since the invading species is rare,  $x_2$  and  $z$  are small. Consequently the rate at which species 2 migrants arrive at each patch,  $\alpha_2$ , is also small. Thus all that matters for the initial invasion are the limiting values (for small  $\alpha_2$ ) of the colonization and extinction functions for species 2. By analogy with



**Fig. 10** One example of how initial invasion rate is influenced by  $\bar{c}_1$ , the extinction risk of the invader in type B patches (Model structure as in Fig. 9). The three curves represent three different  $\bar{m}_1$ , migration rates from type B patches, a: 0.8, b: 0.5, c: 0.2. The figure is based on equations 15-18 and parameter values are  $K_2 = 1$ ,  $x_1 = 0.7$ ,  $e_2 = 0.2$ ,  $\bar{c}_1 = 0.1$ ,  $K_1 = 1$ ,  $\bar{c}_1 = 0.05$ ,  $m_2 = 0.5$ .

equations (6) and (7) we assume that  $C(\alpha_1) = K_2 \alpha_1$ ,  $\bar{C}(\alpha_1, x_1) = \bar{K}_2 \alpha_1$ ,  $E(\alpha_1) = \bar{e}_1$  and  $\bar{E}(\alpha_1) = \bar{c}_2$  for small  $\alpha_1$ . During the initial phase of invasion by species 2, the immigration rate of species 1 migrants can be taken as constant and equal to its value at the equilibrium occupancy  $x_1$  of species 1. We thus also assume that the rate at which a Type 2 patch is converted to a Type B patch,  $\bar{c}_1 = \bar{C}_1(m_1, x_1)$ , is constant. Similarly the rate at which a Type B patch converts to Type 2,  $\bar{e}_1 = \bar{E}_1(m_1, x_1)$ , is constant. We now substitute these expressions into equations (10) and (11), express  $\alpha_1$  in terms of  $x_1$  and  $z$  (eq. 1.2), and since  $x_2$  and  $z$  are small ignore terms involving  $x_1^2$ ,  $x_2^2$  and  $z^2$ . The rate of change in proportion of invaded patches early in the invasion process are then given by the following linearised equations

$$\frac{dx_1}{dt} = (K_2(1 - x_1)m_2 - (e_2 + \bar{c}_1))x_1 + (K_2(1 - x_1)\bar{m}_2 + \bar{c}_1)z$$

$$\frac{dz}{dt} = (\bar{K}_2 x_1 m_2 + \bar{c}_2)x_1 + (\bar{K}_2 x_1 \bar{m}_2 - (\bar{c}_1 + \bar{c}_2))z$$

These equations can be written as

$$\frac{dx_2}{dt} = Ix_2 + Jz \quad (13)$$

$$\frac{dz}{dt} = \bar{J}x_2 + \bar{I}z \quad (14)$$

where

$$I = K_2(1 - x_1)m_2 - (e_2 + \bar{c}_1) \quad (15)$$

$$\bar{I} = \bar{K}_2 x_1 \bar{m}_2 - (\bar{c}_1 + \bar{c}_2) \quad (16)$$

$$J = K_2(1 - x_1)\bar{m}_2 + \bar{c}_1 \quad (17)$$

$$\bar{J} = \bar{K}_2 x_1 m_2 + \bar{c}_2 \quad (18)$$

The quantity  $I$  is the net rate at which a Type 2 patch leads to the production of Type 2 patches;  $J$  is the rate of colonization of empty patches by migrants from the Type 2 patch (i.e.,  $K_2(1 - x_1)m_2$ ) minus the rate of disappearance of the focal Type 2 patch as a result of extinction or colonization by species 1 (i.e.,  $e_2 + \bar{c}_1$ ) (see eq. (15)). The term  $J$  can be interpreted as the rate of "crossing over": the rate at which a Type B patch contributes to the formation of Type 2 patches. There are two ways this contribution is made. The term  $K_2(1 - x_1)\bar{m}_2$  is the rate at which migrants from the Type B patch convert empty patches into Type 2 patches by colonization, and  $\bar{c}_1$  is the rate at which the focal Type B patch itself changes to a Type 2 patch as a result of the extinction of the species 1 occupants (see eq. (17)).

Similarly,  $\bar{I}$  is the net rate at which a Type B patch leads to the production of Type B patches. The quantity  $\bar{K}_2 x_1 \bar{m}_2$  is the rate at which migrants from the Type B patch colonise Type 1 patches, and so convert them to Type B, and  $\bar{c}_1 + \bar{c}_2$  is the rate at which the Type B patch reverts to a patch with just a single species present (eq. 16). The cross term  $\bar{J}$  is the net rate at which a single Type 2 patch contributes to the formation of Type B patches. Again there are two elements to this contribution. Migrants from the Type 2 patch colonise Type 1 patches, and the patch may itself be colonized by species 1 (see eq. 18).

Let  $w = x_1 + z$  be the total proportion of patches in which species 2 is present. To analyse whether species 2 can initially invade we look at how this quantity changes over time. The linearised equations (13) and (14) imply that, whatever the initial values of  $x_1$  and  $z$ , the proportion  $x_2/w$  will settle down to an equilibrium value. As this equilibrium is approached

$$\frac{dw}{dt} \rightarrow \lambda.$$



where the rate of initial invasion  $\lambda$  is the largest eigenvalue of the matrix  $A = \begin{bmatrix} I & I \\ \bar{I} & \bar{I} \end{bmatrix}$ . Thus species 2 can invade the metapopulation if  $\lambda > 0$ , while if  $\lambda < 0$  the species goes extinct in the metapopulation. Figure 10 illustrates how invasion rate can be influenced by the extinction risk of the invader in patches of Type B ( $\epsilon$ ) for one combination of parameter values. In this case increasing extinction risk in Type B patches is very costly for the invader and at too high  $\bar{\epsilon}$ , invasion even becomes impossible (Fig. 10).

Below we shall describe the early invasion process for two special cases, before considering the general criteria for invasion.

#### An 'invisible' invader

Suppose that the invader, species 2, cannot compete for patches with species 1. Specifically species 2 is unable to colonise patches already occupied by species 1, and species 1 immediately wipes out species 2 when species 1 colonises a Type 2 patch. Then there exist no patches containing both species so  $z = 0$ , so that equations (13) and (14) reduce to the single equation

$$\frac{dx_2}{dt} = Ix_2. \quad (19)$$

The rate of growth of the number of patches containing species 2 is just  $I$ , so invasion is possible if  $I > 0$ . If  $x_1$  approaches zero, this expression reduces to the condition for invasion by a single species discussed earlier. As  $x_1$  increases, from (15), there is a value  $< 1$  at which the invader is excluded. In the simple Levins model, for invasion to be possible requires that the invader have a higher equilibrium patch occupancy (were it alone) than does the resident species (see below).

#### A 'parasite type' invader

Now suppose that species 2 is totally reliant on the presence of the native species 1. For example, species 2 might be a parasite or a specialist predator of species 1 (e.g., parasitic wasps are often obligate specialists on particular host species, Nouhuys and Hanski 2002), or an obligate commensal. Specifically assume that species 2 is unable to colonise empty patches. Furthermore, on patches where both species are present (a Type B patch) if species 1 dies out then species 2 immediately dies out as well, so that the patch becomes empty. Then  $x_2 = 0$ , and the rate of growth in the number of patches containing species 2 is just  $I$  since equations (13) and (14) reduce to the single equation

$$\frac{dx_2}{dt} = Ix_2. \quad (20)$$

Thus in this special case invasion is possible if  $\bar{I} > 0$ . From (16), we see that an increase in the occupancy by the resident species 1 tends to facilitate invasion by species 2.

#### General criteria for invasion

We now consider the general case. It is easy to show that if  $I > 0$  then  $\lambda > 0$ , so invasion is guaranteed. This is not surprising: equation (19) shows that even when competition by species 1 is at its strongest, species 2 can invade by just colonising empty patches. A *fortiori*, if  $I > 0$ , species 2 can invade whatever the form of the interaction between the two species. Similarly,  $\bar{I} > 0$  implies  $\lambda > 0$ ; if the invader were able to spread when restricted to patches occupied by species 1, then it is certainly a successful invader, regardless of its performance by itself when confronted with empty patches.

Thus, either  $I > 0$  or  $\bar{I} > 0$  is sufficient to ensure that species 2 can invade. However, when  $I < 0$  and  $\bar{I} < 0$  it may still be possible for species 2 to invade because Type B and Type 2 patches tend to enhance each others formation. In other words migrants from Type 2 patches may colonise Type 1 patches and so convert them to Type B, and Type 2 migrants from Type B patches may colonise empty patches and so convert them to Type 2. It is easy to show that when  $I < 0$  and  $\bar{I} < 0$  species 2 can invade ( $\lambda > 0$ ) provided that  $I/\bar{I} > I$ .

#### Invasion in the long run

We now look at a special case, illustrating how the metapopulation system can develop in the long run, after the initial invasion. We are especially interested in characterizing the conditions for long-term coexistence of the invader and the native species.

Consider the example when two species can only colonise empty patches, so that there are no patches with both species present. Who ever comes first wins the patch (a so called 'lottery model'). Thus the presence of one species reduces the number of patches that are available for the other species to occupy. (Note, however, that so far as a species is concerned it is not simply as if the metapopulation as a whole had fewer patches present. This is because migrants of the species still settle on patches at random, so those migrants that settle on a patch currently occupied by the other species are lost. Thus there is a dilution of migrants that settle on empty patches.) When the two species locally exclude one another the equations governing metapopulation dynamics (which are now just equations (9) and (10)) reduce to

$$\frac{dx_1}{dt} = C_1(\alpha_1)(1 - (x_1 + x_2)) - E_1(\alpha_1)x_1 \quad (21)$$

$$\frac{dx_1}{dt} = C_1(\alpha_1)(1 - (x_1 + x_2)) - E_1(\alpha_1)x_1 \quad (22)$$

For simplicity of exposition we assume that when only species 1 is present there is a unique equilibrium level of patch occupancy, which we denote by  $\hat{x}_1$ . Similarly when species 2 is present alone it has a unique equilibrium level of patch occupancy  $\hat{x}_2$ .

To analyse the ability of each species to invade when the other is present we assume that  $C_1(\alpha_1) \approx K_1\alpha_1$  and  $E_1(\alpha_1) \approx e_1$  for small  $\alpha_1$ , and  $C_2(\alpha_2) \approx K_2\alpha_2$  and  $E_2(\alpha_2) \approx e_2$  for small  $\alpha_2$ ; note that these functions may deviate from this form when  $\alpha_1$  and  $\alpha_2$  are not small. Motivated by Levins' model we define

$$\hat{x}_1 = 1 - \frac{e_1}{K_1 m_1} \quad \text{and} \quad \hat{x}_2 = 1 - \frac{e_2}{K_2 m_2} \quad (23)$$

These are the equilibrium levels of single species occupancy when the above approximations for small  $\alpha_1$  and  $\alpha_2$  hold exactly for all  $\alpha_1$  and  $\alpha_2$ . When  $x_1$  is small we have  $C_1(\alpha_1)(1 - (x_1 + x_2)) - E_1(\alpha_1)x_1 \approx K_1 m_1(\hat{x}_1 + x_2)x_1$ . Thus by equation (21)

$$\frac{dx_1}{dt} > 0 \Leftrightarrow \hat{x}_1 > x_2 \quad \text{when } x_1 \text{ is small.} \quad (24)$$

That is the initial rate of increase in patch occupancy by species 1 is positive if the patch occupancy it initially seems to aim towards in the absence of species 2 ( $\hat{x}_1$ ) is higher than the current patch occupancy by the other species ( $x_2$ ). Thus if species 2 is at its equilibrium of patch occupancy  $x_2^*$ , species 1 can invade if

$$\hat{x}_1 > x_2^* \quad (25)$$

Similarly if species 1 is at its equilibrium of patch occupancy  $x_1^*$ , then species 2 can invade if

$$\hat{x}_2 > x_1^* \quad (26)$$

If both expressions (25) and (26) hold, one will see robust coexistence, in that each species can increase when it is rare and the other species is at its respective equilibrium (see further below).

#### The dynamics of the lottery model with Levins functions

In analysing the possibility for coexistence it is of utmost importance to consider the shape of the extinction and colonization functions. The lottery model outlined

above has been shown to exclude coexistence (Hanski 1999; see also Shurin *et al.* 2004). However, this conclusion is based on assuming Levins' static functions. When each of the single species metapopulations are as in Levins' basic model we have  $C_1(\alpha_1) = K_1\alpha_1$  and  $E_1(\alpha_1) = e_1$  for all  $\alpha_1$ , and  $C_2(\alpha_2) = K_2\alpha_2$  and  $E_2(\alpha_2) = e_2$  for all  $\alpha_2$ . In this special case  $\hat{x}_1 = x_1^*$  and  $\hat{x}_2 = x_2^*$  (i.e. the equilibrium patch occupancy is equal to what is expected by the rate of initial invasion.) Thus if species 2 is at its equilibrium species 1 can invade if and only if  $x_1^* > x_2^*$ . Similarly, if species 1 is at its equilibrium occupancy then species 2 can invade if and only if  $x_2^* > x_1^*$ . Thus the species with the highest equilibrium patch occupancy when alone can invade the other, and it is never possible for both species to be able to invade each other. Figure 11 shows the metapopulation dynamics in the whole of the  $(x_1, x_2)$  plane. As can be seen, the metapopulation dynamics leads to the inevitable extinction of the species with the smallest equilibrium patch occupancy on its own. Thus, with these assumptions, coexistence is not possible, and the species with the largest equilibrium occupancy excludes the other (Hanski 1999 p. 118).

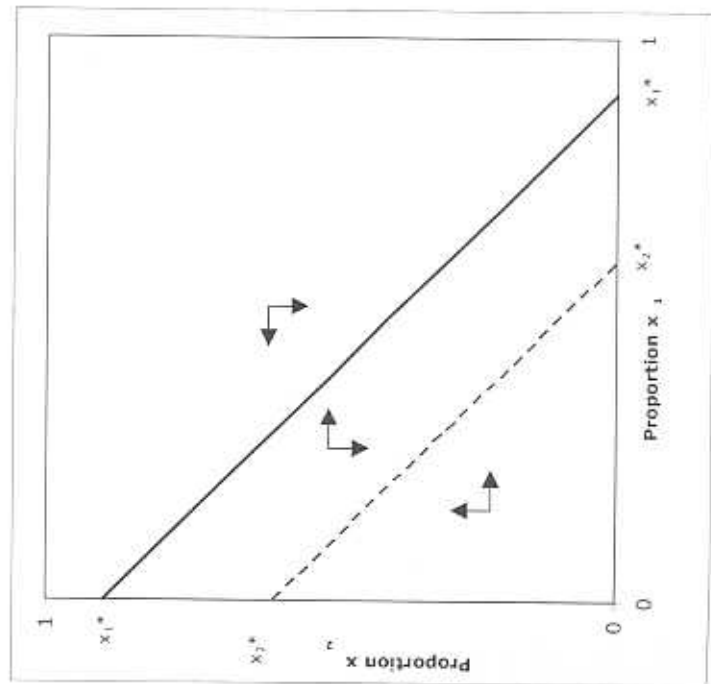


Fig. 11 In a lottery model parameterised with Levins' static functions coexistence of species 1 ( $x_1$ -axis) and species 2 ( $y$ -axis) is not possible. The proportion of patches occupied by species 1 will continue to increase until species 2 goes extinct.

*The lottery model with general functions*

To analyse metapopulation dynamics in the general case when the colonization and extinction rate can have many different shapes we consider how the signs of

$$\frac{dx_1}{dt} \quad \text{and} \quad \frac{dx_2}{dt} \quad \text{vary in the } (x_1, x_2) \text{ plane. When species 2 is absent } (x_2 = 0) \text{ patch}$$

occupancy of species 1 increases with time when occupancy is below the equilibrium occupancy  $\hat{x}_1$ ; i.e.,

$$\frac{dx_1}{dt} > 0 \Leftrightarrow x_1 < \hat{x}_1 \quad \text{when } x_2 = 0 \quad (27)$$

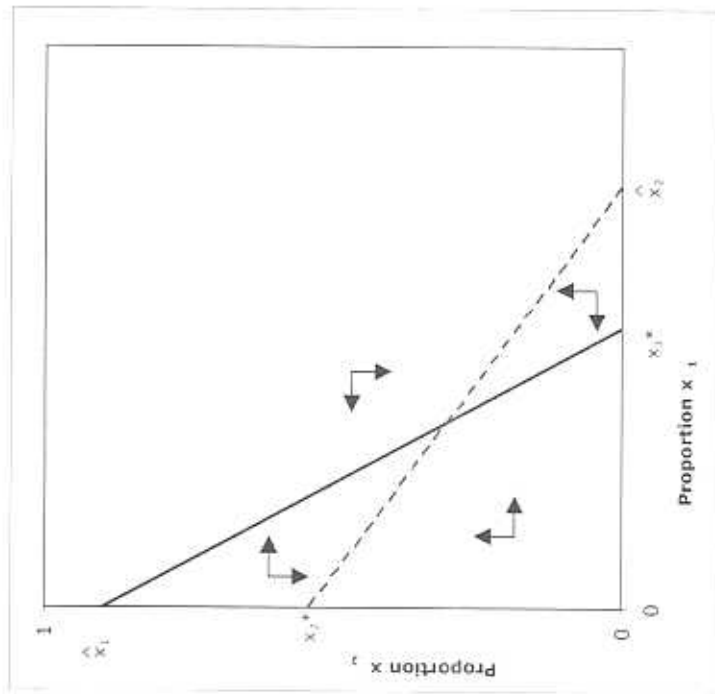
From criteria (27) and (24) the curve

$$\frac{dx_1}{dt} = 0 \text{ in the } (x_1, x_2) \text{ plane joins the point } (x_1^*, 0) \text{ to the point } (0, \hat{x}_1).$$

Similarly the curve  $\frac{dx_2}{dt} = 0$  joins the point  $(\hat{x}_2, 0)$  to the point  $(0, x_2^*)$ .

These curves are illustrated in Fig. 12. The figure also shows the resulting metapopulation dynamics. From criteria (25) and (26), and as the figure illustrates, if  $x_1 > \hat{x}_1$  and  $x_2 > x_2^*$  then each species can invade the other at the latter's equilibrium patch occupancy. The metapopulation dynamics then leads to stable co-existence of the two species. The conditions for mutual invasion can be satisfied when the initial rate of increase in patch numbers is higher than would be expected from its equilibrium. This phenomenon is likely to arise if extinction rate is initially lower or colonization initially higher compared to the rate at higher patch occupancies. This type of disproportionately high initial rate of increase in patch occupancy will be found in populations with anti-rescue effects and/or anti-Allee effects. When such effects are present, the initial rate of increase of each single species metapopulation can be high without a correspondingly high patch occupancy at equilibrium. This reduced equilibrium size reduces competition, allowing co-existence, even in the lottery model (see Fig. 12).

The dynamics and stability of a two-species system depend on the exact shape of the colonization and extinction functions. We have illustrated this for the simple lottery model; more complex forms of interactions among species require further analysis.



**Fig. 12** A lottery model which allows different shapes of the C and E functions can have stable coexistence of two species. The initial rate of invasion must be disproportionately high, which can be the case for example when there is an anti-rescue effect.

**EXPLICIT SPATIAL STRUCTURE AND FINITE NUMBER OF PATCHES**

The framework described above assumes the number of patches to be very large. However, if the number of patches is less than about 100 (Hanski 1999, p. 56), single stochastic events of colonization and extinction become important. The risk that all patches will go extinct simultaneously (metapopulation extinction) depends on the combination of metapopulation size and the shape of the per patch extinction function (Fig. 7). A consideration of the effects of finite patch numbers is inevitable when considering the consequences of explicit space and landscape structure.

A very active area of research at present is focused on making metapopulation theory spatially explicit. The basic idea is that in a metapopulation with a finite number of patches each patch has its own specific characteristic and landscape position, which in turn influence its probability of extinction and likelihood of colonization. Metapopulation dynamics of the entire ensemble reflects both heterogeneity among patches (e.g., in area, which can influence extinction) and the specific landscape structure and pattern of connectivity of the patches. The size



and composition of local populations also influence invasion speed (Neubert and Caswell 2000). Ovaskainen and Hanski (2004) provide an excellent overview of recent theory in this area, and here we simply sketch some of the basic issues, with an emphasis upon implications for invasion biology. Metapopulation models with a spatially explicit structure provide important linkages with landscape ecology, and with applied issues such as population viability analyses.

One biological assumption that is built into the generalized Levins model we have considered above is that all empty patches are accessible to migrants emigrating from all occupied patches. In general, dispersal is spatially limited, and so this assumption will be violated. This may be particularly important to consider in the early stages of an invasion, when a colonising species has established a beachhead on just one or a few sites. From these initial sites, with limited dispersal there may be a small, finite number of empty sites available for colonization. Mathematically, the dynamics can be described as a Markov chain (in discrete time) or Markov process (in continuous time). Extinction can arise because of an analogue of demographic stochasticity at the metapopulation scale. Even if initial invasion is successful, the rate of increase (and rate of spatial spread) of the colonising species can be damped, because many colonists emerging from the center of the invasion simply move to patches that are already occupied. In reaction-diffusion style models of invasive species, heterogeneity in dispersal rates seems to exert a particularly strong effect on the overall rate of invasion of species (Shigesada and Kawasaki 1997). In spatially-explicit landscape models, there can be critical thresholds in habitat connectivity, below which species are likely to go extinct, even though a substantial number of patches exist which are perfectly suitable for occupancy (With 2002). We might call this the 'Tantalus effect' in metapopulation ecology (after the Greek legend of Tantalus, who was tormented by an eternity of hunger and thirst, with luscious grapes and clean water visible, but just barely out of reach....).

In general, spatially explicit metapopulation models seem to imply that localised dispersal makes invasion more difficult. However, were one to place the generalized Levins model discussed above into a spatially explicit landscape, a richer array of outcomes might be observed. For instance, with Allee effects, given uniform dispersal over a large number of patches from an initial propagule, too few individuals might enter any given patch to ensure successful colonization. If instead dispersal is localised, most individuals might enter the same, relatively few patches, thus increasing the effective migrant density in those patches. This could facilitate colonization. What one might observe in this case is a successful nucleus of initial colonization, followed by accretionary growth as neighboring patches get successfully colonized. Alternatively, if there are gaps in availability of suitable habitats, Allee effects could lead to constraints on the ability of an invasive species to expand much beyond the sites of its original colonization (Keitt *et al.* 2001).

One complication that arises in spatially-explicit metapopulations is that if there is heterogeneity among patches (e.g., in attributes that influence

colonization), such heterogeneity is likely to exhibit spatial autocorrelation. This can lead to population synchrony which can strongly influence the probability of regional extinction (i.e., a failed invasion) (Caswell and Cohen 1995, Engen *et al.* 2002). In general, for population persistence the size of the metapopulation should be substantially greater than the scale at which such population synchrony is observed. Working out the implications of spatial and temporal autocorrelation for metapopulation dynamics is an important area for future work.

#### EMPIRICAL STUDIES AND THE ROLE OF THEORY

In attempts to 'test' predictions from theoretical models, empirical metapopulation biologists almost without exception will reach the conclusion that their study system does not fit the assumptions of the model. Or, they might express it the other way around — the model does not fit their observations. But there are many uses of theoretical models, and not all models are meant to be tested. One of their main functions is as tools for thought. Such models can be used to expose the logic of processes assumed to be operating in particular systems, showing clearly how predictions depend on assumptions. Theoretical models can be used as a starting point to generate questions about empirical systems, and as new biological knowledge about the driving forces of that system are discovered, new simplistic general models can be developed, or new more detailed models can be elaborated. Occasionally a model might predict the behaviour of a system (Box 2), although stochasticity due to weather and the chaotic dynamics of nature will mostly hide such correspondence. However, models are useful if correctly handled: incorporating mechanisms that we think are important can reveal the potential behaviour of a system. Just as in learning about the simple building blocks of hydrology and gas kinetics, meteorologists also learn more about the nature of currents and winds and even climate change, and yet are unable to predict the weather at a certain spot more than a few days ahead, so the mismatch between a theoretical model and empirical systems in ecology rarely provides sensible 'tests' of the theory itself.

Metapopulation theory in the generalized form presented here is a philosophical tool that highlights how species can persist despite the fact every single sub-population faces a substantial extinction risk. It does not attempt to describe the detailed behaviour of a given real system at a given time, but captures essentials of forces that apply to real systems.

For example, Gutierrez *et al.* (2001) studied the spatial distribution of four lepidopteran butterfly species. Because the four species all had the same favourite host plant (*Lotus corniculatus*) the authors claimed this must be a system where the predictions from multi-species models would be realised. However, it turned out that environmental factors other than the favourite host plant determined the distribution of the four species (for example; alternative host plants, differences between coastal or inland sites, and vulnerability to grazing). One of the species

was present in the entire landscape and might not act as a metapopulation at all. The study claims to have proven that the assumptions of phenomenological multi-species metapopulation models are unrealistic. But these models can only provide interesting insights into systems where several species actually do compete for the same patches, and where colonization-extinction dynamics and interspecific interactions are in fact major forces at work. These assumptions need to be assessed, and it is not clear that the empirical system of Gutierrez *et al.* (2001) provides a good match to the metapopulation assumption. We suggest that on *a priori* grounds it is reasonable to believe that there are multi-species assemblages which quite faithfully match the assumptions of metapopulation theory (e.g., aquatic predators and prey in ponds occupy patches which may dry and suffer extinctions, parasites in the same host can interact and all go extinct when the host dies, etc.) and where multi-species metapopulation models are likely to produce some interesting insights.

The old Popperian view that hypothesis must be confirmed or falsified in critical tests has led to much confusion at the interface between theoretical and empirical metapopulation biology. Theoretical models can not say more than 'given exactly these conditions we will get this or that outcome; they can not be validated or falsified in systems with other conditions and other prevailing mechanisms. It would be like telling the meteorologists that they should be skeptical about the proposition 'warm air is less dense than cold air', simply because they cannot accurately predict today's rainfall in a specific location, such as Ullapool.

## Box 2

### *Biological control experiment in a snail metapopulation living in ponds in Guadeloupe*

*Biomphalaria glabrata* is a native snail species that is the intermediate host for human intestinal schistosomes (a trematode infection). A Venezuelan snail *Marisa cornuarietis* was introduced in 1987. The invader destroyed local populations of water lilies that are important habitats for the native *B. glabrata*. A strong decline in patch occupancy in the *B. glabrata* metapopulation followed in the ponds where the competitor was introduced. Interestingly, nearby control ponds (without the introduced competitor) also had declining patch occupancy (Poirtier *et al.* 2004). Although the authors state that environmental circumstances might have contributed to the decline of *B. glabrata* in the un-invaded control ponds, they point out that the observed pattern matches that predicted by simple theoretical metapopulations models — lower patch occupancy leads to lowered overall colonization rate, and the whole metapopulation network can be affected by the removal of a few patches.

## CONCLUSION

We have summarised some aspects of how generalized metapopulation theory is relevant for understanding invasions into patchy habitats. When species survive in a landscape as a metapopulation it is critical that colonization success is higher than the extinction rate of subpopulations. In conservation the worry is often that an invader competes with a native species. We have refined a two-species metapopulation model to capture different kinds of interactions, including competition. There is a full range of behaviours that emerge, depending on the type of colonization and extinction function of the invader, and the type of influence of the native species. The existence of Allee and anti-Allee effects opens up a rich variety of possible dynamical outcomes. The invasive species becomes extinct if its initial success in colonizing empty patches or resisting extinction in occupied patches at low patch number is too low; we have suggested a number of particular mechanisms that can lead to such exclusion. If the initial growth rate is positive, it can become established and coexist sustainably with the native species or force the latter to go extinct. If the invasive species competes for resources this can reduce patch occupancy for the native species and if the native species is vulnerable, and has an unstable equilibrium beyond which there is no return, then extinction of the native species can be sudden and difficult to reverse. We predict metapopulation theory will become significant more refined and applied to study invasive species problems.

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## REFERENCES

- Allee, W. C. 1931. Animal aggregations: a study in general sociology. Chicago University Press, Chicago.
- Amarsékar, P. 2003 Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* **6**, 1109–1122.
- Bangyeekhun, E. 2002. Parasites on crayfish. Characterisation of their pathogenesis host interactions and diversity. Acta Universitatis Upsalensis. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 737. 46 pages.
- Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445–449.
- Caswell, H. and J. Cohen. 1995. Red, white and blue: environmental variance spectra and coexistence in metapopulations. *Journal of Theoretical Biology* **176**, 301–316.
- Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities

- and their role in community stability and organization. *American Naturalist* **122**, 661-696.
- Engen, S., R. Lande and B. -E. Saether. 2002. The spatial scale of population fluctuations and quasi-extinction risk. *American Naturalist* **160**, 439-451.
- Gomulkiewicz, R. and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? *Evolution* **49**, 201-207.
- Gotelli, N. J. and W. G. Kelly. 1993. A general model of metapopulation dynamics. *Oikos* **68**, 36-44.
- Gutiérrez, D., J. L. León-Cortés, R. Menéndez, R. J. Wilson, M. J. R. Cowley and C. D. Thomas. 2001. Metapopulations of four lepidopteran herbivores on a single host plant, *Lotus corniculatus*. **82**, 1371-1286.
- Gyllenberg, M., I. Hanski and A. Hastings. 1997. Structured metapopulation models. Pages 93-122 in Hanski, I. and M. E. Gilpin, eds. *Metapopulation Biology*. Academic Press, London.
- Harding, K. C. and J. M. McNamara. 2002. A unifying framework for metapopulation dynamics. *American Naturalist* **160**, 173-185.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**, 210-221.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**, 151-162.
- Hanski, I. 1999. *Metapopulation Ecology*. Oxford University Press, Oxford.
- Hanski, I. and M. Gyllenberg. 1993. Two general metapopulation models and the core-satellite species hypothesis. *American Naturalist* **142**, 17-41.
- Holt, R. D. 1997. From metapopulation dynamics to community structure. Pages 149-164 in I. Hanski and M. E. Gilpin, eds. *Metapopulation Biology*. Academic Press, San Diego.
- Holt, R. D. and J. H. Lawton. 1993. Apparent competition and enemy-free space in insect host-parasitoid communities. *American Naturalist* **142**, 623-645.
- Holt, R. D. and T. Keitt. 2000. Alternative causes for range limits: a metapopulations perspective. *Ecology Letters* **3**, 41-47.
- Holt, R. D. 2002. Food webs in space: On the interplay of dynamic instability and spatial processes. *Ecological Research* **17**, 261-273.
- Hoopes, M. F., R. D. Holt and M. Holyoak. 2005. The effects of spatial processes on two-species interactions. Page: 35-67. In *Metacommunities: Spatial Dynamics and Ecological Communities*, eds. M. Holyoak, M. A. Leibold and R. D. Holt. U. of Chicago Press, Chicago.
- Keitt, T. H., M. A. Lewis and R. D. Holt. 2001. All-se effects invasion pinning and species borders. *American Naturalist* **157**, 203-216.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**, 624-635.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237-240.
- Levins, R. and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the Natl. Academy of Sciences, USA*, **68**, 1246-1248.

- MacArthur, R. H. and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton.
- Neubert, M. and H. Caswell. 2000. Demography and dispersal: calculations and sensitivity analysis of invasion speed for structured populations. *Ecology* **81**, 1613-1628.
- Nee, S. and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* **61**, 37-40.
- Nouhuys, S. V. and I. Hanski. 2002. Colonisation rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. **71**, 639-650.
- Ovaskainen, O. and I. Hanski. 2004. Metapopulation dynamics in highly fragmented landscapes. Pages 73-104 in I. Hanski and O. E. Gaggiotti, editors. *Ecology, Genetics and Evolution of Metapopulations*. Elsevier/Academic, Burlington.
- Pointier, J. P. and P. David. 2004. Biological control of *Biomphalaria glabrata*, the intermediate host of schistosomes, by *Marisa cornuarietis* in ponds of Guadeloupe: long term impact on the local snail fauna and aquatic flora. *Biological Control* **29**, 81-89.
- Rolán-Alvarez, E., K. Johannesson and J. Erlandsson. 1997. The maintenance of a clone in the marine snail *Littorina saxatilis*: the role of home site advantage and hybrid fitness. *Evolution* **51**, 1838-1847.
- Saceri, L., M. Kuussaari, M. Kankare, P. Viikman, W. Fortelius and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**, 491-494.
- Schöps, K. 1999. Effect of deforestation on the spatial dynamics of an endangered weevil species. Page 45 in *Habitat Loss Helsinki*, 7-12 Sept. Hakapaino Oy, Helsinki.
- Shigesada, N. and K. Kawasaki. 1997. *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford.
- Shurin, J. B., P. Amaresekare, J. M. Chase, R. D. Holt, M. F. Hoopes, R. Law and M. A. Leibold. 2004. Alternative stable states and regional community structure. *Journal of Theoretical Biology* **227**, 359-368.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**, 196-218.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ.
- With, K. A. 2002. Using percolation theory to assess landscape connectivity and effects of habitat fragmentation. Pages 105-130 in K. J. Gutzwiller, editor. *Applying Landscape Ecology in Biological Conservation*. Springer-Verlag, New York.