

Metapopulation persistence in fragmented landscapes: significant interactions between genetic and demographic processes

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Abstract

We formulated a mathematical model in order to study the joint influence of demographic and genetic processes on metapopulation viability. Moreover, we explored the influence of habitat structure, matrix quality and disturbance on the interplay of these processes. We showed that the conditions that allow metapopulation persistence under the synergistic action of genetic and demographic processes depart significantly from predictions based on a mere superposition of the effects of each process separately. Moreover, an optimal dispersal rate exists that maximizes the range of survival rates of dispersers under which metapopulation persists and at the same time allows the largest sustainable patch removal and patch-size reduction. The relative impact of patch removal and patch-size reduction depends both on matrix quality and the dispersal strategy of the species: metapopulation persistence is more affected by patch-size reduction (patch removal) for low (high)-dispersing species, in presence of a low (high) quality matrix. Avoidance of inbreeding, through increased dispersal when the rate of inbreeding in a population is large, has positive effects on low-dispersing species, but impairs the persistence of high-dispersing species. Finally, size heterogeneity between patches largely influences metapopulation dynamics; the presence of large patches, even at the expense of other patches being smaller, can have positive effects on persistence in particular for species of low dispersing ability.

Introduction

Habitat fragmentation is recognized to have major effects on species persistence due in particular to the isolation between population fragments (Davies *et al.*, 2001), which has negative demographic and genetic consequences (Gaggiotti & Hanski, 2004).

Dispersal of individuals between habitat patches can have positive effects on the long-term persistence of fragmented populations, a process known as the rescue effect. Populations can be rescued demographically, as immigrant individuals increase the size of the recipient

population (Casagrandi & Gatto, 1999, 2002a) or, genetically, as migration can result to a significant reduction of inbreeding depression (Saccheri *et al.*, 1998; Richards, 2000; Couvet, 2002).

However, emigration could lead to a demographic deficit, due to the mortality of emigrant individuals during dispersal, which may not be compensated by immigration. The intensity of this phenomenon is mediated by the resistance of the matrix, i.e. the nonhabitat portion surrounding habitat patches, to interpatch movement: the increased mortality of dispersers within a low-quality matrix can contribute significantly to patch isolation and, therefore, increase the probability of extinction (Vandermeer & Carvajal, 2001).

The fact that the matrix is an adverse habitat for the species is a common phenomenon (Hanski & Ovaskainen, 2000), in particular when the matrix is a

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human-dominated area. In such a case, the low survival of dispersing individuals can be for example due to negative effects of agriculture on wildlife – associated with pesticides and/or the rarity of palatable food – or hunting (Donald & Evans, 2006; see also Woodroffe & Ginsberg, 1998, for large carnivores).

Species at higher trophic levels and with large body sizes can be especially vulnerable to the loss of emigrants within the matrix for two main reasons (Ewers & Didham, 2005). First, the usually low reproductive rates of these species cannot compensate the high mortality during dispersal resulting to declining populations. Second, these species have high requirements in terms of habitat area and are, consequently, more heavily affected by isolation. A single patch, which would be large enough to maintain a minimum viable population – supposed to amount to a thousand of individuals (Lande, 1995) – will be impossible to find, except in few areas in the world; see the example of grizzly bears in Yellowstone (Miller & Waits, 2003).

Hence, the outcome of these antagonistic effects, and consequently the dispersal rates that allow metapopulation persistence, would jointly depend on the state of the matrix, the structure and the size of suitable patches as well as the biological characteristics of the species (e.g. reproductive rate and dispersal ability; With, 2004).

Although impressive efforts have been made to model metapopulation dynamics, there is still a clear dichotomy in the factors being taken into account. On the one hand, studies analysing the effects of disturbances on metapopulations in relation to the size and the growth rate of the populations (Hastings & Wolin, 1989), patch quality (Hanski, 1994), matrix quality (Vandermeer & Carvajal, 2001) or all of these factors together (Casagrandi & Gatto, 1999) neglect the genetic effects of fragmentation, while on the other hand, studies exploring the genetic processes associated with fragmentation do not usually incorporate demographic and habitat considerations (Mills & Allendorf, 1996; Couvet, 2002; Glémin *et al.*, 2003). Higgins & Lynch (2001) investigated the interaction of environmental, genetic and demographic stochasticity on metapopulation persistence. They showed that the incorporation of deleterious mutations accumulation changes significantly the predictions concerning the influence of dispersal and metapopulation structure on metapopulation persistence. However, they did not include in their model the effects of matrix quality, i.e. the consequences from the imbalance between emigration and immigration.

Our study is an attempt for a more synthetic view that explores the interplay of demographic and genetic processes in relation to habitat and matrix structure. We begin by assuming that both habitat patches and the matrix are homogeneous. Population dynamics within a habitat patch is modelled as the outcome of reproductive potential of the species and the balance between emigration and immigration. These demographic processes are influenced

by underlying genetic processes, i.e. fitness depends on the frequency of deleterious mutations, and the dispersal rate may change according to the level of inbreeding within patches (referred to as avoidance of inbreeding). Patch and matrix quality are reflected on the carrying capacity of habitat patches and the survival rate of dispersing individuals respectively.

In order to highlight the synergistic action of demographic and genetic processes on metapopulation persistence, we compare our conclusions with the predictions of two models that consider each process separately: (i) a deterministic demographic model (Casagrandi & Gatto, 2002b), which ignores both the effects of inbreeding on population growth rate and the relationship between inbreeding and dispersal; and (ii) an infinite island model, widely used in theoretical genetic studies (Couvet, 2002; Whitlock, 2002; Glémin *et al.*, 2003) that ignores the imbalance between emigration and immigration.

We then explore the consequences of heterogeneity in habitat patches. Heterogeneity can have contrasting effects on metapopulation dynamics (Ewers & Didham, 2005). For instance, Day & Possingham (1995) showed that according to the colonization rate, the variability in patch size can either decrease or increase the probability of metapopulation extinction relative to an equal patch-size metapopulation.

Finally, our model allows us to examine the relative influence of different types of habitat disturbance (e.g. removal of entire patches vs. reduction in patch size) on metapopulation persistence. Useful conclusions for the conservation of fragmented populations are extracted.

Model description

Metapopulation description

We assume that habitat fragmentation creates a network of habitat patches. Patches may differ in area and/or quality, and both differences are reflected on carrying capacity, K_i , $i = 1, \dots, p_{\max}$, where p_{\max} is the number of different types of patches. Each type of patch consists of n_i identical patches ($i = 1, \dots, p_{\max}$); in what follows, we assume that $n_i \rightarrow \infty$, $\forall i$. We modelled metapopulation structure according to the island model, i.e. all patches of a given type are equally distanced; the distance, d_{ij} ($i \neq j$), between different types of patches may, however, differ from the distance between patches of the same type, d_{ii} . More precisions can be found in a latter section where we detail the dispersal process.

We first build a general model of an arbitrary large number of patch types and then limit our attention to two simple cases where there are only one or two kinds of patches.

Life cycle within patches

Populations are randomly mating and grow in discrete generations, with a simple form of density dependence

following mutation, selection, reproduction and dispersal each generation.

We denote $N_i(t)$ as the expected size of populations of type i ($i = 1, \dots, p_{\max}$) at generation t and $\lambda_i(t)$ the population growth rate prior to dispersal. Em_i is the number of emigrants from i -type patches and Im_{ij} the number of immigrants coming from populations occurring in j -type patches and ending up in populations occurring in i -type patches. The population growth rate prior to dispersal, $\lambda_i(t) = RW_i(t)$, depends on the net reproductive rate, R , i.e. the number of progeny per surviving adult per generation, which we assumed to be constant over generations; in other words, R is the reproductive rate for individuals carrying none of the segregating deleterious alleles. $W_i(t)$ is the mean population fitness (i.e. mean survival until reproduction), which is a function of the frequency of deleterious alleles. In order to estimate the mean population fitness, one has to calculate the frequency of the deleterious alleles and the genetic differentiation between populations (Whitlock, 2002); this is done in the following paragraphs. If, following dispersal, the population size exceeds carrying capacity, the population size is reset to the carrying capacity.

Hence, the expected population size in a patch of type i in the next generation will be:

$$N_i(t+1) = \min \left\{ \lambda_i(t)N_i(t) - Em_i + \sum_{j=1, \dots, p_{\max}} Im_{ij}, K_i \right\} \quad (1)$$

Dispersal

Island model. The expected number of emigrants per habitat patch of type i is:

$$Em_i = \lambda_i(t)N_i(t)\delta_i(t) \quad (2)$$

where $\delta_i(t)$ is the dispersal rate of patch i .

Dispersal between patches implies that emigrants must pass through the unsuitable habitat (the matrix). The proportion of emigrants from a patch of type j who reach successfully a patch of type i is determined by the survival rate during dispersal and the landing rate in each type of patch.

First, the survival rate during dispersal, S_{ij} , depends on (i) the quality of the matrix, a low-quality matrix implies high mortality during dispersal; and (ii) the distance between patches, d_{ij} ; more distant patches will lead to a lower proportion of emigrants surviving during dispersal. We assumed a similar relationship as in Hanski & Ovaskainen (2000):

$$S_{ij} = e^{-\alpha d_{ij}}, \quad (3)$$

where $1/\alpha$ can be interpreted as the mean distance that a disperser travels before dying and depends on the quality of the matrix. The exponential distribution has often been shown to fit well data collected on distance travelled during dispersal for a variety of taxonomic groups (Murrell *et al.*, 2002).

The landing rate of emigrants in a suitable habitat, Q_{ij} , i.e. the rate at which dispersers from a patch of type j will settle in a patch of type i , depends on (i) the distance between source and target patches, d_{ij} ; (ii) the area of the target patch, A_j ; we assumed that the area of a patch is proportional to the carrying capacity: $A_i/A_j = K_i/K_j$; and (iii) the number of i -type patches, n_i . According to our model, dispersal is more likely to closer, larger and more frequent types of patches. We assumed the following relationship for the landing rate:

$$Q_{ij} = \frac{n_i A_i e^{-\alpha d_{ij}}}{\sum_{l=1, \dots, p_{\max}} n_l A_l e^{-\alpha d_{il}}} \quad (4)$$

Hence, the mean number of immigrants coming from j -type patches and ending up in i -type patches is:

$$Im_{ij}(t) = \lambda_j(t)N_j(t) \frac{\delta_j(t)}{n_i} n_j S_{ij} Q_{ij} \quad (5)$$

We allow dispersal to increase with increasing inbreeding, as found in many vertebrates (Berger, 1987; Bjørnstad *et al.*, 1998). A simple way to express this relation is: $\delta_i(t) = \delta[1 + \beta f_i(t)]$, where δ corresponds to the intrinsic dispersal rate, β is a positive coefficient, constant by assumption, and $f_i(t)$ the inbreeding coefficient of populations occurring in i -type patches. Note that inbreeding in our model refers to generalized inbreeding linked to small population sizes and not to lack of panmixia due to consanguineous mating system.

Overall, the expected population size in a patch of type i in the next generation can be expressed as:

$$N_i(t+1) = \min \left\{ \lambda_i(t)N_i(t)[1 - \delta_i(t)] + \frac{1}{n_i} \sum_{j=1, \dots, p_{\max}} \lambda_j(t)N_j(t)\delta_j(t)n_j S_{ij} Q_{ij}, K_i \right\} \quad (6)$$

Two patch types

To study the effect of patch heterogeneity, we will restrain, for simplicity, our analysis to metapopulations consisting of two types of patches at maximum. The two types consist of equal number of patches and patches are evenly distributed in space within each type, i.e. $d_{ij} = d_{ii} = d_{jj} = d$. We assumed that variation in patch quality is reflected on differences in carrying capacity.

In the case of two-patch types, population size is given as follows:

$$N_i(t+1) = \min \left\{ \lambda_i(t)N_i(t)[1 - \delta_i(t)(1 - S_{ii}Q_{ii})] + \lambda_j(t)N_j(t)\delta_j(t)S_{ij}Q_{ij}, K_i \right\}, \quad (7)$$

where $S_{ij} = e^{-\alpha d}$ and $Q_{ij} = A_i/(A_i + A_j)$, with $i, j = 1, 2$.

Population genetics

We considered two alleles per locus model, A being the wild-type allele and a a deleterious and partially recessive allele. The relative fitness of the AA , Aa and aa genotypes

at a given locus are 1, $1 - hs$ and $1 - s$ respectively, where s is the selection coefficient and h the dominance coefficient of the deleterious allele. We assume that mutations at different loci act independently and multiplicatively.

Population inbreeding coefficient

The genetic differentiation between populations occurring in i -type patches can be expressed by F_{STi} (Crow & Kimura, 1970). Due to the infinite number of patches considered in our model, individuals from different populations can be reasonably assumed to be genetically unrelated. Hence, the genetic differentiation between populations is equal to the inbreeding coefficient within each population: $f_i = F_{STi}$ (Wright, 1969).

The change in the inbreeding coefficient, and consequently in F_{STi} , between two consecutive generations is given by:

$$F_{STi} = f_i(t+1) = \left[\frac{1}{2N_i(t)} + \left(1 - \frac{1}{2N_i(t)}\right) f_i(t) \right] \times \left[1 - \sum_{j=1, \dots, n} \text{im}_{ij}(t) \right]^2 \quad (8)$$

Equation 8 gives the rate of inbreeding for neutral alleles, while the calculation of mean population fitness requires the rate of inbreeding for deleterious alleles. However, both rates of inbreeding are close when the deleterious effects are weak (small s), the case studied here (Whitlock, 2002).

Frequency of deleterious alleles, $q_i(t)$

After reproduction, the expected frequency of deleterious alleles over all patches of type i is $q'_i(t) = q_i(t) + \Delta q_{\text{mut}} + \Delta q_{\text{sel}}$, where Δq_{mut} and Δq_{sel} are the changes in allele frequency due to mutation and selection respectively. If μ is the mutation rate from allele A to a , then (Whitlock, 2002):

$$q'_i(t) \approx q_i(t) + \mu(1 - q_i(t)) - q_i(t)s \frac{1 - F_{STi}(t)}{1 + F_{STi}(t)} ((1 - h)F_{STi}(t) + h) \quad (9)$$

Equation 9 holds when we consider recurrent mutation and a large number of patches as in our model (Whitlock, 2002). Notice that the effect of migration between patches of type i on the expected allele frequency is taken into account through its impact on F_{STi} .

If $\text{im}_{ij} = \text{Im}_{ij}(t)/N_i(t+1)$ is the fraction of immigrants in i -type patches at time $t+1$, which are coming from j -type patches, then:

$$q_i(t+1) = (1 - \text{im}_{ij})q'_i(t) + \text{im}_{ij}q'_j(t), \quad i \neq j \quad (10)$$

with

$$\text{im}_{ij} = \frac{\lambda_j(t)N_j(t)\delta_j(t)S_{ij}Q_{ij}}{\lambda_i(t)N_i(t)[1 - \delta_i(t)] + \sum_{j=1, \dots, n} \lambda_j(t)N_j(t)\delta_j(t)S_{ij}Q_{ij}} \quad (11)$$

Average fitness, $W_i(t)$

Assuming multiplicative fitness across loci, the average fitness over all populations in patches of type i will be (Whitlock, 2002):

$$W_i(t) = [1 - \text{sq}_i(t)(2h + (1 - 2h)F_{STi}(t))]^L, \quad (12)$$

where $q_i(t)$ is the expected frequency of deleterious alleles over all i -type populations and L is the number of selected loci.

Initial conditions

We assumed that initial populations are issued from a large population at selection–mutation balance. Hence, when fragmentation occurs, the frequency of deleterious alleles is $q_i(0) \approx \mu/(\mu + hs)$, and the growth rate is $\lambda_i(0) = RW(0) \approx R(1 - 2\mu)^L$ (Crow & Kimura, 1970). The initial size of i -type populations is set to carrying capacity, $N_i(0) = K_i$. Individuals are assumed to be initially unrelated and the genetic differentiation between populations to be zero ($F_{STi}(0) = f_i(0) = 0$).

The values of the genetic parameters used ($U = 1$, $\bar{s} = 0.02$, $\bar{h} = 0.35$) correspond to empirical estimations for *Drosophila* sp. (Lynch *et al.*, 1995, Lynch *et al.*, 1999). However, there is still much controversy about the genomic rate of mutations affecting fitness. The variation in the mutation rate is documented both within and between species, with U ranging from 0.01 to above 1. In a recent review article, Baer *et al.* (2007), based on recent studies, concluded that 'it seems likely that U is rarely much less than 1 in multicellular organisms, and in certain taxa (for example, primates) it is probably substantially greater than 1' (see Baer *et al.*, 2007 for further explanations and examples).

We, therefore, investigate two sets of parameters for deleterious mutations (Table 1). The mutant effect is assumed to follow a gamma distribution with shape parameter β and mean effect \bar{s} . The values considered are in accordance with previous investigations (see for instance, Deng & Lynch, 1996; Garcia-Dorado, 2003; Fernandez *et al.*, 2004). The dominance coefficient of mutations were obtained from an exponential function of the gene effects, $h = e^{-ks}/2$ (Deng & Lynch, 1996), where k is a constant allowing the mean dominance coefficient to be the desired one. To examine the outcome of mutations with variable effects, we proceeded as in Couvet (2002).

One single type of patches

To explore the interaction between genetic and demographic processes, we apply the previous model for the

Table 1 Sets of parameters for deleterious mutations.

	U	\bar{s}	\bar{h}	β
Model I	1	0.02	0.35	1
Model II	0.06	0.264	0.25	2.3

case of a single kind of patches. In this case, population size is given by:

$$N(t+1) = \min\{RW(t)N(t)[1 - \delta(t)] + \lambda(t)N(t)\delta(t)S, K\}, \quad (13)$$

and the genetic differentiation between populations is given by:

$$F_{STi} = f_i(t+1) = \left[\frac{1}{2N_i(t)} + \left(1 - \frac{1}{2N_i(t)}\right) f_i(t) \right] [1 - \text{im}(t)]^2, \quad (14)$$

where $\text{im}(t) = \frac{\delta(t)S}{1 - \delta(t) + \delta(t)S}$.

For simplicity, we drop all the subscripts since $i = 1$ of eqn 5; in particular there is one landing rate, in this case, $Q_{11} = 1$.

Equation 13 shows that the population size has only two asymptotic values, $N = 0$ or K , according to whether the population asymptotic growth rate is less or more than unity. Thus, the relationship $RW(t)[1 - \delta(t) + \delta(t)S] = 1$ defines the persistence–extinction boundaries. To find these boundaries, we iterated the system of eqns 9, 10, 13 and 14 until the population size reaches equilibrium. We considered that equilibrium was attained if the population growth rate, $RW(t)[1 - \delta(t) + \delta(t)S]$, remains the same for a 1000-generation period.

Simple demographic and genetic model

We will now see the assumptions of two simple models: (i) a deterministic demographic model (Casagrandi & Gatto, 2002b), which ignores both the effects of inbreeding on population growth rate and the relationship between inbreeding and dispersal; and (ii) an infinite island model, which ignores the imbalance between emigration and immigration. In the Results, we compare the predictions of these models with the single patch-type demogenetic model described above.

Demographic model

According to the demographic model, both the growth rate and the dispersal rate are constant over time. Hence, eqn 6 is reduced to:

$$N(t+1) = \min\{R(1 - 2\mu)^L(1 - \delta(1 - S))N(t), K\} \quad (15)$$

We, thus, obtain the single persistence–extinction boundary: $R(1 - 2\mu)^L[1 - \delta(1 - S)] = 1$. This condition states that extinction occurs when the number of immigrants and the intrinsic growth rate cannot compensate the loss of emigrants within the matrix.

Genetic model

We considered a genetic model, according to which population size remains constant over generations, i.e. $N(t) = K$. In this case, extinction occurs when the population growth rate drops below unity, as in Lynch

et al. (1995), i.e. $RW(t) < 1$. We take, therefore, a single persistence–extinction boundary corresponding to $RW^* = 1$, with W^* being the asymptotic mean population fitness calculated by eqn (12).

Patch removal and patch-size reduction

Our definition of patch removal is the random destruction of a fraction X_i of i -type patches. In our model, patch removal results to an increase in the mean distance between patches: $d'_{ij} = d_{ij}/(1 - X_i)$, where d_{ij} (d'_{ij}) is the distance between two different types of patches before (after) patch destruction.

The increase in distance between patches leads to a decrease in the probability of finding a suitable patch before dying. First, the survival rate during dispersal will decrease, as follows:

$$S'_{ij} = e^{-\frac{ad_{ij}}{1-X_i}} \quad (16)$$

Second, the landing rate can also be altered due to patch loss. This rate depends not only on the proportion of destroyed habitat but also on the species ability to recognize suitable patches. We explored the cases of active and passive dispersal according to whether emigrants avoid or not destroyed patches.

In the case of passive dispersal, emigrants will keep going to destroyed patches. Hence, emigrants from the $(1 - X_i)n_i$ remained patches will continue to disperse towards n_i destinations. Hence, when patch loss is coupled with passive dispersal, eqn 6 becomes:

$$N_i(t+1) = \min\left\{ \lambda_i(t)N_i(t)[1 - \delta_i(t)] + \frac{1}{n_i} \sum_{j=1, \dots, p_{\max}} \lambda_j(t)N_j(t)\delta_j(t)n_j(1 - X_j)S_{ij}Q_{ij}, K_i \right\} \quad (17)$$

Habitat alteration can also take the form of patch erosion, i.e. a fraction of the original patch, denoted as Y , becomes unsuitable for the species. Patch-size reduction decreases, therefore, both the area and the carrying capacity of the original patches from A_i and K_i to $(1 - Y)K_i$ and $(1 - Y)A_i$ respectively.

Results

One single type of patches

Persistence–extinction boundaries

The simple demographic model predicts an upper persistence–extinction boundary, i.e. the metapopulation persists for dispersal rates lower than that indicated by the persistence–extinction boundary (Fig. 1). Hence, completely isolated populations with initially positive growth rates would not go to extinction, as we considered that

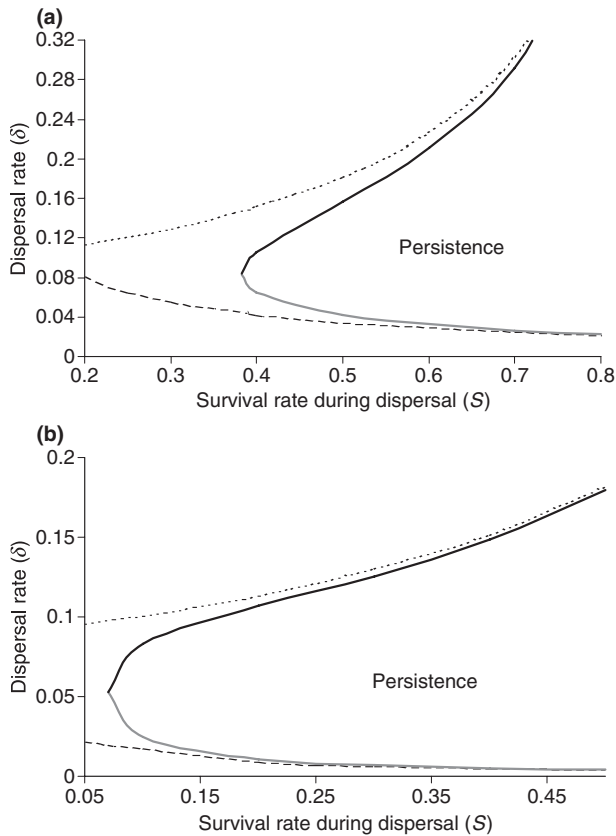


Fig. 1. Persistence–extinction boundaries in relation to dispersal rate, δ , and emigrant survival rate, S , according to (i) the demogenetic model (solid lines), (ii) the demographic model (dashed black line) and (iii) the genetic model (broken black line). The metapopulation persists below the black curves and above the grey ones. The metapopulation consists of one type of patches with carrying capacity, $K = 100$. The initial growth rate of local populations is $\lambda_0 = 1.1$. The dispersal rate does not depend on the inbreeding level ($\beta = 0$). The set of mutation parameters correspond to (a) Model I and (b) Model II. For the assumptions of these models see Table 1.

demographic stochasticity is not a cause of extinction in the present model.

The genetic persistence–extinction boundary corresponds to the minimal dispersal rate that ensures metapopulation persistence (Fig. 1). Below this minimum, genetic load is too high for the population to persist.

In contrast, the demogenetic model predicts two persistence–extinction boundaries in the parameter space of the dispersal rate, δ , and the survival rate during dispersal, S ; the metapopulation persists when the values of the pair (δ, S) lie between the two boundaries (Fig. 1).

The comparison of the two simple models with the demogenetic model shows that boundaries that result from the superposition of the two simple models yield a larger area for metapopulation viability than that predicted by the demogenetic model, which takes into

account the synergistic effects of demography and genetics on metapopulation dynamics.

Another important point is that the range of dispersal rates that allow metapopulation persistence decreases as the survival rate of emigrant individuals decreases. As a consequence, there is a survival rate for which the two dispersal rates, minimal and maximal, coincide. This induces impossibility of persistence at lower emigrant survival rates, whatever the dispersal rate is. Hence, the intersection of the two persistence–extinction boundaries determines an ‘optimal’ dispersal rate in the sense that this rate maximizes the range of survival rates of dispersers under which metapopulation persists.

The set of parameters for deleterious mutations assumed has a significant influence on metapopulation persistence, i.e. for a low mutation rate (Fig. 1b), the range of (δ, S) values that allow persistence increases significantly. Moreover, the optimal dispersal rate decreases moderately (0.083 and 0.053 for Models I and II respectively). However, even when low mutation rates are considered, the difference between the boundaries of the demogenetic model and those predicted by the two simple models still exists, although less pronounced.

Dependence of the dispersal rate on the level of inbreeding

If we allow dispersal rate to increase with the level of inbreeding, to avoid the deleterious effects of generalized inbreeding, the persistence–extinction boundaries shift towards lower dispersal rates (Fig. 2). Hence, inbreeding avoidance can be beneficial for low-dispersing species but unfavourable for high-dispersing ones.

However, inbreeding avoidance has a low effect on metapopulation persistence even for a substantial increase in dispersal rates with inbreeding (e.g. $b = 10$).

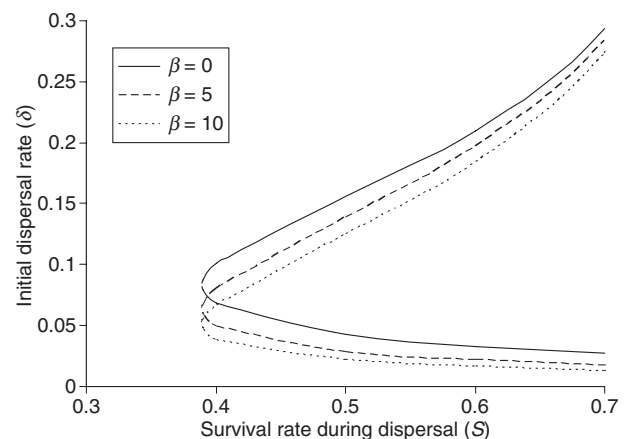


Fig. 2. The effects of inbreeding avoidance on metapopulation persistence. Persistence–extinction boundaries according to the demogenetic model for various values of β , where β quantifies the dependence of dispersal rate on the rate of inbreeding ($\delta_i(t) = \delta[1 + \beta f_i(t)]$). The set of mutation parameters is according to Model I.

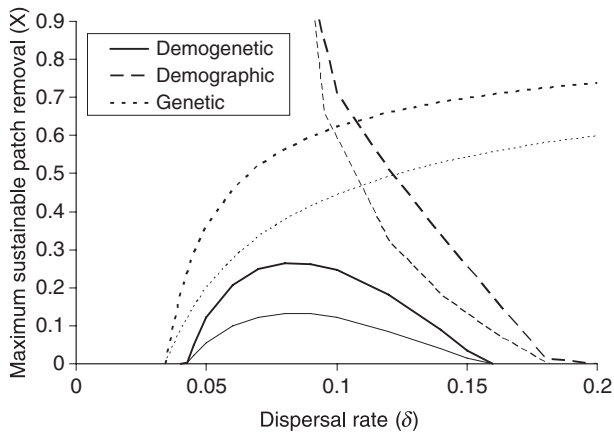


Fig. 3. Maximum sustainable patch removal in relation to dispersal rate, δ when (i) emigrants avoid destroyed patches (thick lines) and (ii) emigrants keep going to destroyed patch (thin lines). The emigrant survival rate is set to $S = 0.5$ and the carrying capacity of the remaining patches to $K = 100$. The set of mutation parameters is according to Model I.

Moreover, the minimum survival rate during dispersal that allows metapopulation persistence is identical to the case of constant dispersal rates.

Consequences of patch removal and patch-size reduction
Nonavoidance of destroyed patches strongly limits the maximal sustainable patch removal. Hence, patch removal would induce a great risk of extinction for species that disperse passively (Fig. 3).

Moreover, the maximal sustainable patch removal depends on the dispersal rate. The idea of the 'optimal' dispersal rate, as defined in the previous section, is further supported by these results as the largest proportion of sustainable patch removal occurs for dispersal rates that correspond to the optimal rate.

Once again, the predictions from the juxtaposition of the simple demographic and genetic models depart significantly from the predictions of the demogenetic model; the maximum sustainable patch removal is significantly lower when the synergistic effects of demography and genetics are considered (Fig. 3).

We investigated the relative effects of patch removal and patch-size reduction, when the proportion of lost patches equals the fraction of eroded habitat per patch, i.e. $X = Y$ (Fig. 4). Although both disturbances have strong detrimental effects on metapopulation persistence, patch removal is, in most cases, more harmful than habitat erosion. However, for low dispersal rates and high survival rates during dispersal, the relative influence of habitat erosion and loss of entire patches is inverted.

In Fig. 4, dispersal is active, i.e. emigrants avoid destroyed patches. As expected, the negative impact of patch removal on metapopulation persistence is more prominent when dispersers keep going to destroyed patches (results not shown).

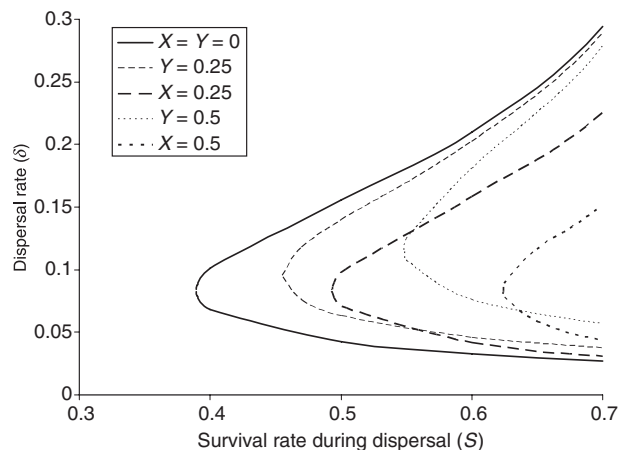


Fig. 4. Persistence–extinction boundaries in relation to dispersal rate, δ , and the emigrant survival rate, S , for various intensities of patch removal and habitat erosion. Three values for the fraction of eroded habitat out of the original habitat are considered: $Y = 0$ (no erosion), 0.25, 0.5. The same values are considered for the fraction of entirely destroyed patches ($X = 0, 0.25, 0.5$). Emigrants are assumed to avoid destroyed patches. The metapopulation consists of one type of patches with carrying capacity $K = 100$. In the case of habitat erosion carrying capacity decreases to $(1 - Y)K$. The set of mutation parameters is according to Model I.

Influence of patch heterogeneity on metapopulation persistence

In order to highlight the effects of size heterogeneity between patches on metapopulation persistence, we explored a simple case according to which habitat patches consist of two types that differ in their carrying capacity.

Variance in patch-carrying capacity has two opposing results on metapopulation dynamics. On the one hand, it can increase the persistence area, particularly for low dispersal rates (Fig. 5). Patch heterogeneity implies the presence of larger patches, which show lower extinction rates under conditions of isolation. On the other hand, heterogeneity between patches lowers mean metapopulation size, because, in contrast to one patch-type metapopulations, heterogeneous patches can have intermediate population sizes ($0 < N < K$). This is due to smaller patches that show intermediate densities and act as sinks, whereas migrants coming from large patches prevent them from vanishing.

The same pattern was observed when the values of mutation parameters were according to Model II (results not shown). However, the differences between homogeneous and heterogeneous patches are slighter.

Discussion

We studied the synergistic effects of demographic and genetic processes (loss of migrants within the matrix and genetic isolation between fragments) as well as of habitat

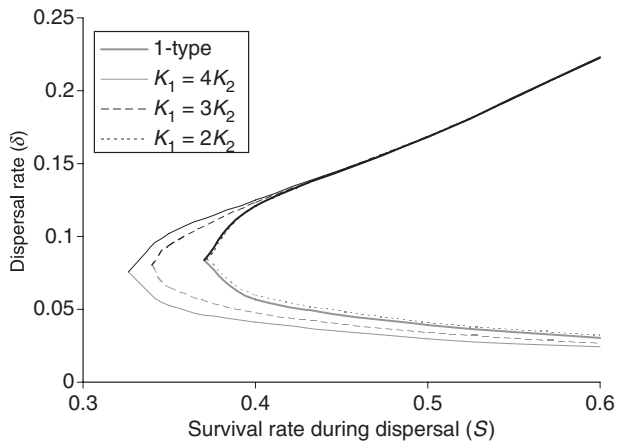


Fig. 5. Influence of patch heterogeneity on metapopulation persistence. The figure shows the persistence–extinction boundaries in the plane (δ, S) , when the metapopulation consists of two types of patches equidistant from one another ($d_{12} = d_{11} = d_{22}$). Carrying capacities are set so as $(K_1 + K_2)/2 = K$, where K is the carrying capacity in the case of one type of patches; in the example, $K = 100$. Survival during dispersal between patches is set to $S_{11} = S_{12} = S_{22} = 0.5$. Initial growth rates are set to $\lambda_1 = \lambda_2 = 1.1$ for both types. The set of mutation parameters is according to Model I.

characteristics, such as the quality of the matrix and the carrying capacity of suitable patches, on metapopulation persistence.

Our results underline the importance of considering the interaction between demographic and genetic processes. A mere superposition of the persistence–extinction areas obtained separately by the simple genetic and demographic models does not correspond to the persistence–extinction boundaries predicted by the demogenetic model. This is particularly so in a low-quality matrix where the synergistic action of the imbalance between emigration and immigration and the genetic deterioration due to isolation lead to metapopulation extinction, which is not predicted by the two simple models. Overall, the conditions of metapopulation persistence are significantly narrower than predicted by the superposition of the two simple models.

Optimal dispersal rate

A general result suggested by our study is that metapopulation persistence requires intermediate dispersal rates. As a consequence, both low- and high-dispersing species would face a great risk of extinction due to habitat fragmentation. Low dispersal leads to metapopulation extinction due to genetic isolation between habitats. In consistency with the study of Couvet (2002), the minimal dispersal rate for persistence, without loss of individuals during emigration, is about one individual per population per generation. For some threatened

species, the dispersal rate is lower than this minimum (Colas *et al.*, 1997; Gibbs *et al.*, 1997), suggesting that genetic isolation is a factor of metapopulation decline. In highly dispersing species, extinction may occur due to a demographic effect: the loss of emigrants within the matrix can be higher than the excess of individuals that results from reproduction, leading to population decline until ultimate extinction.

The range of dispersal rates that allows metapopulation persistence depends strongly on the quality of the matrix, i.e. the survival rate during dispersal; a reduction in matrix quality increases the set of low and frequent dispersers to be eliminated. For a sufficiently low survival rate during dispersal, this range reduces to a single dispersal rate, which can be defined as the optimal dispersal rate. The optimal dispersal rate maximizes the range of survival rates under which metapopulation persists or, in other words, minimizes the influence of variations in matrix quality on metapopulation persistence. Moreover, the optimal dispersal rate allows both the largest sustainable patch removal and the higher sustainable reduction in patch size.

Overall, a species dispersing according to the optimal dispersal rate should maximize its chances to persist in the presence of disturbances, whether these imply degradation in the matrix quality or habitat characteristics (patch erosion or removal).

Effects of inbreeding avoidance on metapopulation persistence

There is strong evidence that dispersal can be selected for to avoid the detrimental effects of inbreeding (Lambin, 1994; Dobson *et al.*, 1997). Our results suggest that the increase in dispersal rates with the level of inbreeding has positive effects on the metapopulation persistence for low-dispersing species that suffer most from the deleterious effects of inbreeding. However, a remarkable result is that for high-dispersing species, a negative effect of such a relationship occurs. In this case, inbreeding avoidance triggers a further loss of emigrants within the matrix and increases, therefore, the populations' demographic deficit; the positive effects of inbreeding avoidance on fitness and, hence, on reproductive output, cannot counterbalance this further loss of migrants.

Consequences of habitat disturbance: patch removal and patch-size reduction

Our study underlines the importance of species ability to recognize suitable patches on metapopulation persistence; if emigrants keep trying to settle in destroyed patches, the metapopulation resistance to patch removal decreases significantly. Hence, active dispersal is of particular importance for the persistence of species, such

as large mammals, that suffer from a great loss of suitable habitat (Ceballos & Ehrlich, 2002).

The relative impact of patch erosion and patch removal depends on the quality of the matrix and the dispersal rate. For highly dispersing species and/or low matrix quality, patch removal can be far more harmful than habitat erosion. Conversely, for low-dispersing species, and low rates of emigrant loss within the matrix, patch erosion can be more detrimental. In this case, the size of local populations is only moderately regulated by immigration or emigration. Thus, population persistence depends on the population intrinsic rate of increase, which is a function of the deleterious allele frequency; patch-size reduction will lead to adverse genetic effects (higher inbreeding and genetic load), changing an expanding population to a decreasing one.

Consequences of size heterogeneity between patches

We explored the effects of size heterogeneity between patches on metapopulation persistence by comparing two landscapes with the same total areas, where one of the landscapes has all patches with equal areas and the other consists of patches of two different sizes.

Our results suggest that species inhabiting landscapes with heterogeneous patch sizes show a larger range of dispersal rates that allow metapopulation persistence. In other words, patch heterogeneity favours metapopulation persistence. Furthermore, heterogeneity has more pronounced effects for species with poor dispersal abilities. These results highlight the importance of large patches, which show low extinction probabilities under conditions of strong isolation and can act as sources of immigrants.

However, size heterogeneity between patches can reduce the metapopulation capacity because small patches act as sinks, due to the interplay of demographic and genetic processes, and therefore show intermediate densities.

The important role of heterogeneity has been supported by many authors, who have concluded that spatial features, such as connectivity of patches, patch size and dispersal, are essential to understand metapopulation dynamics (Day & Possingham, 1995; Hanski, 1998; Xu *et al.*, 2006). Xu *et al.* (2006), who used a spatially realistic Levins model, also concluded that heterogeneous patch sizes result to metapopulations of stronger persistence. However, incorporating local population dynamics allows us to observe the antagonistic effects of patch heterogeneity on metapopulation dynamics, i.e. although heterogeneity increases dispersal conditions that allow persistence, it decreases the metapopulation capacity. Taking into account environmental and demographic stochasticity might therefore moderate the positive effects of heterogeneity.

Perspectives

Although we considered populations with low growth rates, such as found for mammals (Mills & Smouse, 1994), an optimal intermediate dispersal rate should also occur for species with high growth rates, but for alternative reasons. In their case, the loss of emigrants within the matrix should have a minor effect on metapopulation viability. However, substantial dispersal is likely to synchronize population dynamics, leading to metapopulation inviability due to increased stochasticity at the metapopulation level (Earn *et al.*, 2000). Hence, an advantage for medium dispersers should also occur for species with a high growth rate.

A comment is also needed for the values of the mutation parameters used in our study. Although strong arguments are advanced in favour of the values we used (Lynch *et al.*, 1999; Baer *et al.*, 2007), recent studies argue that the rate of mutation per diploid genome could be significantly lower than $U = 1$ (Fry *et al.*, 1999; Bataillon, 2000). A decrease in U has two effects: first, it allows the metapopulation to persist for lower survival rates during dispersal and, second, reduces, although moderately, the value of the optimal dispersal rate.

Another issue of importance is the possibility of evolutionary rescue, i.e. that the evolution of dispersal, in response to a modification of the environment (e.g. patch-size reduction), could improve metapopulation resistance to such modification. Hence, it is important to know under what conditions there will be selection for higher (or lower) dispersal rates compared to what we defined as an optimal dispersal rate. The dispersal rate has indeed been shown to evolve rapidly in response to habitat changes (Thomas *et al.*, 2001). Notice, however, that the response in terms of dispersal rates to recent fragmentation may be inefficient to ensure persistence: many constraints could prevent the metapopulation from responding optimally to landscape changes, such as the interaction between local adaptations and dispersal (Colas *et al.*, 2004).

Finally, the matrix clearly determines metapopulation dynamics and further investigation of its potential effects is of great importance for the conservation of metapopulations. Further development of the present model would help to consider the relative impact of stochasticity and deterioration, in the matrix and in the habitat occupied. Obviously, metapopulation viability depends on processes in both areas, and metapopulation management will require comparing their joint impact on both the occupied habitat and the matrix.

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