

Interim Report

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Evolution of Migration Rate in a Spatially Realistic Metapopulation Model

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The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physico-chemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

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Abstract

We use an individual-based, spatially realistic metapopulation model to study the evolution of migration rate. We first explore the evolutionary consequences of habitat change in hypothetical patch networks on a regular lattice. If the primary consequence of habitat change is an increase in local extinction risk due to decreased local population sizes, migration rate increases. A non-monotonic response, with migration rate decreasing at high extinction rate, was obtained only by assuming very frequent catastrophic extinctions. If the quality of the matrix habitat deteriorates, leading to increased mortality during migration, the evolutionary response is more complex. As long as habitat patch occupancy does not decrease markedly with increased migration mortality, reduced migration rate evolves. However, once mortality becomes so high that empty patches remain uncolonized for long time, evolution tends to increase migration rate, which may lead to an ‘evolutionary rescue’ in a fragmented landscape. We examined in detail the role of kin competition in explaining our results. Kin competition has a quantitative effect on the evolution of migration rate in our model, but the patterns described above are primarily caused by spatio-temporal variation in fitness and mortality during migration. We apply the model to real habitat patch networks occupied by two checkerspot butterfly (*Melitaea*) species, for which sufficient data are available to rigorously estimate most of the model parameters. The migration rate predicted by the model is not significantly different from the empirically observed one. Regional variation in patch areas and connectivities leads to regional variation in the optimal migration rate, predictions which can be quantitatively tested with appropriate empirical data.

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Evolution of Migration Rate in a Spatially Realistic Metapopulation Model

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Introduction

Evolution of migration rate is one of the better studied topics in evolutionary ecology (Gadgil 1971, Comins et al. 1980, Olivieri and Gouyon 1997), inspired by the wide range of migration rates and patterns exhibited by animals and plants. A large number of explanations based on both group and individual selection arguments for more or less migration, which may be unconditional or conditional on the state of the individual or its environment, has been put forward in the literature (reviewed by Johnson and Gaines 1990, McPeck and Holt 1992, Gandon and Michalakis 2000, Ronce et al. 2000b).

Recently, the selection that increasing loss and fragmentation of natural habitats may impose on the evolution of migration rate has received much attention (Leimar and Norberg 1997, Travis and Dytham 1998, 1999). Given the various costs and benefits of migration and the various types of habitats (ephemeral or stable), it is not obvious which way habitat fragmentation might select migration rate to evolve. According to one view, high migration rate leads to elevated mortality, and as migration mortality is likely to increase with increasing habitat fragmentation, a lower migration rate is expected to evolve. According to an opposing view, high migration, which is a prerequisite for long-term metapopulation survival in a fragmented landscape, is likely to increase when the environment becomes increasingly fragmented, extinction rate increases, and an increasing fraction of suitable habitat is unoccupied and available for exploitation. In this situation, high migration rate may evolve, even if mortality during migration might be high (Comins et al. 1980). From the individual perspective, risk of mortality during migration may be more than balanced by a chance of finding an uncrowded patch with little or no competition, favoring increased migration rate. On the other hand, increased migration can be either beneficial or detrimental for metapopulation survival.

These two viewpoints relate to two extreme situations that are well documented for natural populations. If there is just a single isolated population living in a stable habitat, selection is expected to operate against emigration from that population. Accordingly, populations on isolated oceanic islands and mountaintops tend to show low migration rate and capacity (Hesse et al. 1951, Roff 1990). In the other extreme, only species with high migration rate may survive in ephemeral habitat patches with fast turnover. Rare species that occur in naturally patchy or fragmented habitats have indeed high migration rates (Brown 1951, Southwood 1962, Roff 1994).

With human-caused habitat fragmentation, the situation is less clear-cut, and an appropriate model is required to take into account the relevant biology of the species and the key features of landscape structure. Some general models of the evolution of migration assume an infinite number of habitat patches, no explicit spatial structure in the landscape,

and recolonization that occurs immediately following population extinction (e.g., Gandon and Michalakis 1999, Ronce et al. 2000a). In this case, colonization is effectively decoupled from migration and the model should be used cautiously to draw inferences about the consequences of habitat fragmentation on the evolution of migration rate. In other models, migration is modelled on a regular lattice, with random movements between the neighboring lattice cells (Travis and Dytham 1998, 1999). Such models implicitly assume that migrating individuals have no power to actively search for suitable habitat, unlike the myriads of animal species that inhabit naturally patchy habitats.

Studies of the evolution of migration rate have been mostly based on general models that necessarily make many simplifying assumptions. Though such models have definite advantages, they also have the drawback that producing testable quantitative predictions is difficult or impossible. It may also be difficult to ascertain to what extent the results are sensitive to the simplifying structural assumptions made in the model.

In this paper, we have adopted a more specific modeling approach complementing an expanding body of empirical literature. Many recent metapopulation studies have documented the dynamics of species living in highly fragmented landscapes, which can be described as irregularly-spaced networks of patches of unequal size (Hanski 1998, 1999). Much of this work has been done on butterflies (Thomas and Hanski 1997), which is also the focal taxon in our study. In particular, we take advantage of two empirically-based models to parameterize a submodel for the movements of adult individuals among habitat patches and to parameterize long-term metapopulation dynamics. To these models, we add an individual-based simulation to model the evolution of migration rate. Individual-based models are often plagued by many untested assumptions and parameters, but this is not the case here because of the wealth of information available for the focal species, making it possible to rigorously parameterize the two sub-models with empirical data. To some extent, our model can be used to test the robustness of the predictions of previous simpler models.

We start by describing the model and how it has been parameterized for the butterfly metapopulations. Comparable models can be constructed for other species with different spatial population structure and different life histories by modifying relevant model parameters or assumptions. The result section is divided into two parts. The purpose of the first part is to study more general questions about the evolution of migration rate in response to habitat loss and fragmentation by assuming a simple lattice structure for the landscape. These results also allow us to compare the behavior of our model with the behavior of other models. In the second part we demonstrate how the model can be applied to butterfly metapopulations living in real fragmented landscapes to generate testable quantitative predictions.

Individual-based model

In this section we describe the evolutionary model and its components. The backbone of the model is a description of the life cycle of the focal species. If the model were to be applied to other species, the first task would be to make the necessary modifications in the description of the life cycle in the simulation model. Being a model of the evolution of migration rate, a key component of the model is a submodel of the movement behavior of individuals (adult individuals in the case of butterflies). For this purpose we use a previously described statistical model that can be parameterized with empirical mark-release-recapture data. This submodel covers only the migration period in one generation. In our evolutionary model, we have to model the long-term dynamics. To ensure that our

model predicts realistic long-term dynamics, we tune some parameter values such that our individual-based evolutionary model produces similar year-to-year dynamics than a previously parameterized ecological metapopulation model. We thus require the evolutionary model to be ecologically realistic. Having thus constructed the model, we allow one parameter, the propensity to migrate, to evolve, while other parameters are fixed to the values estimated from empirical data. We now turn to a description of the model components and the way it was parameterized for the focal taxa in this study.

Life history model

The model assumes the following life cycle which corresponds closely with the life cycle of the Glanville fritillary butterfly (*Melitaea cinxia*) and related checkerspot butterflies (Kuussaari 1998, Hanski 1999). These species are the focal taxa to which the model will be applied in the ‘Results’ section. Most of the model parameters can be estimated from data on *M. cinxia*, but the best data on adult movements comes from the related species *Melitaea diamina*, which is ecologically very similar to *M. cinxia* (Wahlberg et al. 1996). All the parameters are summarized in table 1.

We assume a highly fragmented landscape, consisting of discrete patches of suitable habitat surrounded by uniformly unsuitable habitat. There is one generation per year, and the adults, the dispersive stage in the life cycle, hatch in early summer. Females mate only once, and after mating they start to search for host plants suitable for oviposition. The search continues until they die or the season ends after day 30; very few females survive until the end of the season. During the search, females may migrate to another habitat patch. Eggs are laid in large batches, at most one egg batch per day. Each egg batch develops into one larval group. The larvae remain in sib-groups until the next spring, and thus larval group is the demographic unit for most of the year. Survival of the larval groups until autumn is density-dependent because the availability of suitable host plants is limited. We assume that local carrying capacity sets an upper limit to the number of surviving larval groups. If population size is greater than the carrying capacity, random larval groups are removed until the carrying capacity is reached. Below the carrying capacity there are no adverse effects of density dependence. During winter and spring mortality is density-independent.

Migration of adults

Migration is modelled using the virtual migration (VM) model of Hanski et al. (2000). This model consists of a set of structural assumptions about the influence of habitat patch area and isolation on survival and migration (the biological model), and a statistical model for maximum-likelihood parameter estimation from mark-release-recapture data. The model assumes identical and independent individuals, and essentially the purpose is to model the individual capture histories as obtained from a field study. We use the VM model as a well-parameterized sub-model for migration in our individual-based model of the evolution of migration rate.

Here we focus on describing the biological model; the original paper should be consulted for further details and on the method of parameter estimation. The VM model is based on discretized histories of individuals. In the course of unit time, which is one day in our application for butterflies, events are assumed to occur in the following order. First, individuals have a daily within-patch survival probability ϕ before possibly emigrating. Second, surviving individuals have a patch-specific probability of emigrating from patch

Table 1: Model parameters and their values for the checkerspot butterflies. For the migration parameters the 95% confidence intervals are also available. Distances are measured in km and patch areas in ha.

<i>Parameters for larval groups</i>	
Area-dependent carrying capacity (K_i)	$10A_i^{0.5}$ ^a
Mean diapause survival of larval groups (s_w)	0.4 ^b
Between-patch variance in diapause survival ($\sigma_{s_w}^2$)	0.0092 ^c
Correlation in diapause survival (ρ_{s_w})	0.25 ^c
Mean larval group size (f)	12 ^b
k of the negative binomial distribution for larval group size	3 ^c
Within-patch correlation in larval group size (ρ_f)	0.75 ^c
<i>Parameters for the virtual migration model</i> ^d	
Within-patch survival probability (ϕ)	0.890 (0.868–0.935)
Migration propensity (η)	0.130 (0.103–0.176)
Scaling of emigration (ζ_{em})	0.170 (0.000–0.414)
Scaling of immigration (ζ_{im})	0.263 (0.000–0.577)
Distance dependence (α)	4.910 (3.798–6.138)
Migration mortality (λ)	0.175 (0.061–0.517)
<i>Other parameters for adults</i>	
Daily probability of laying an egg batch	0.33 ^e
<i>Technical parameters for evolution of migration rate</i>	
Number of loci	32
Mutation probability per locus	0.001

^a from *M. cinxia*, Hanski et al. (1996)

^b from *M. cinxia*, Kuussaari (1998)

^c no data

^d from *M. diamina*, Hanski et al. (2000)

^e from *M. cinxia*, M. Kuussaari, pers. comm.

j , which is a power function of patch area A_j

$$\epsilon_j = \eta A_j^{-\zeta_{em}}, \quad (1)$$

where ζ_{em} is a scaling constant and parameter η is termed migration propensity. Third, the probability of surviving migration increases with increasing connectivity S_j of patch j , and is given by

$$S_j^2 / (\lambda + S_j^2), \quad (2)$$

where λ is a parameter describing migration mortality: large values result in low survival. Connectivity of patch j is measured by

$$S_j = \sum_{k \neq j} \exp(-\alpha d_{jk}) A_k^{\zeta_{im}}, \quad (3)$$

where d_{jk} is the distance between patches j and k , α scales distance dependence of migration (if $\alpha \gg 0$, distant patches contribute very little to the connectivity of patch j), and ζ_{im} scales patch area dependence of immigration. Probability of arriving at patch k , given

that an individual has emigrated from patch j and survived migration, depends on the contribution of patch k to the connectivity of patch j and is given by $\exp(-\alpha d_{jk})A_k^{\zeta_{im}}/S_j$. Taking mortality into account, the probability of an individual leaving patch j to reach patch k is given by

$$\psi_{jk} = \frac{\exp(-\alpha d_{jk})A_k^{\zeta_{im}}}{\lambda/S_j + S_j}. \quad (4)$$

These probabilities constitute a matrix which is used in the present model to redistribute migrating individuals. Note that the presence of other patches influences ψ_{jk} (via S_j), and hence the model includes 'competition' among the target patches for migrating individuals.

Long-term metapopulation dynamics

For our purposes, it is essential that the individual-based simulation model produces realistic long-term dynamics. To achieve this we used the incidence function model (IFM, Hanski 1994), which has been previously widely applied to butterfly metapopulations (Hanski et al. 1996, Wahlberg et al. 1996, Hanski 1999). The incidence function model is a stochastic patch occupancy model, which incorporates a finite number of patches and spatial variation in patch areas and connectivities. The latter two factors influence, respectively, the rates of population extinction and colonization. For a description of the model and its application see Hanski (1994, 1999), ter Braak et al. (1998) and Moilanen et al. (1998).

Parameterization for checkerspot butterflies

We assume that survival of larval groups in diapause over winter and early spring follows a bell-shaped beta distribution, with the mean survival $s_w = 0.4$, as observed in an intensive study of *Melitaea cinxia* (Kuussaari 1998), and variance $\sigma_{s_w}^2$. To account for regional stochasticity (Hanski 1999), we assume that there is correlation ρ_{s_w} in the survival among populations.

In the spring, shortly before the adults emerge, the average larval group size f in *M. cinxia* is 12 larvae per larval group (Kuussaari 1998). We assume that larval group size follows negative binomial distribution with parameter k . Within-patch correlation in larval group sizes, ρ_f , reflects common factors influencing larval survival, for instance risk of parasitism (Lei and Hanski 1998) and quality of host plants in the habitat patch (Hanski 1999).

Parameter values for the migration submodel have been estimated for *Melitaea diamina* (Table 1; Hanski et al. 2000). During their lifetime, female butterflies are assumed to lay one clutch of eggs with probability 0.33 in each day. This value takes into account that females do not lay at the maximal rate (one clutch per day) unless the environmental conditions are optimal (which they typically are not).

There are four parameters for which empirical estimates are currently unavailable: variance in the survival of larval groups during diapause ($\sigma_{s_w}^2$), between-patch correlation in the survival in diapause and in spring before hatching (ρ_{s_w}), parameter k of the negative binomial distribution describing the sizes of larval groups, and within-patch correlation in the sizes of larval groups (ρ_f). The values of these parameters were chosen within feasible limits in such a manner that the long-term dynamics of the individual-based model were similar to the dynamics predicted by the IFM. The tuning of these free parameters was done by simulating the dynamics of the individual-based model in the real network of 94 patches inhabited by *Melitaea diamina* in the Tampere region in Finland (Wahlberg et al. 1996). This is the same metapopulation from which the parameter estimates for the

Table 2: Comparison of the dynamical properties of the incidence function model (IFM) and the individual-based model for *Melitaea diamina*. The observed occupancy (fraction of occupied patches) in 1995 was 0.37. x and e are the parameters of the extinction risk–patch area relationship, $E_i = eA_i^{-x}$. The values for the IFM are from Wahlberg et al. (1996; the other IFM parameters had the values $\alpha = 1.0$ and $y = 3.62$). For the individual-based model, the values are based on 10 simulation runs of 1100 generations initiated with the observed occupancy pattern and the first 100 generations omitted. The values in parentheses are standard deviations, except for x in the IFM (standard error).

Model	Occupancy	x	e	Turn-overs/yr
Incidence function model	0.36 (0.05)	0.884 (0.257)	0.014	3.7 (0.6)
Individual-based model	0.36 (0.04)	0.973 (0.050)	0.018 (0.003)	8.6 (1.3)

migration submodel were obtained. The carrying capacity is assumed to depend on patch area (in ha) according to the power function $K_i = 10A_i^{0.5}$, where the power is obtained from Hanski et al. (1996) and the coefficient was chosen to yield realistic densities. Simulations were initiated with the observed pattern of patch occupancy.

In selecting the values for the four free parameters, three criteria were used. First, the long-term average patch occupancy should be close to the observed value. Second, extinction risk should scale with patch area as predicted by the IFM. Third, the numbers of extinction and colonization events should be similar to the prediction of the IFM. The following parameterization gave the best fit among a large number of different combinations: $\sigma_{s_w}^2 = 0.0092$, $\rho_{s_w} = 0.25$, $k = 3$ and $\rho_f = 0.75$. These values are consistent with the known biology of the species. With this parameterization, the mean patch occupancy predicted by the individual-based model is very close to the value observed in the field and predicted by the IFM (Table 2). Extinction risk in small patches is somewhat higher in the individual-based model than in the IFM, which results in higher turn-over rate in the former (Table 2). The dynamics of this metapopulation are analyzed in the ‘Results’ section.

Evolutionary dynamics

We assume that migration propensity η (eqn. 1) depends on the genotype of an individual and that inheritance is clonal (haploid). No information exists on the actual genetic architecture of this trait. Because there is no indication of dispersal dimorphism in checkerspot butterflies, we assume that migration propensity is a quantitative trait influenced by many genes of small additive effects. We implement this assumption by representing genotypes as bit strings of 32 bits in length. Each bit corresponds to one locus, with possible alleles ‘0’ and ‘1’. Relatedness between two individuals is calculated as the proportion of loci with shared alleles. Phenotype is given as the sum of ‘1’s in the string, scaled in such a manner that the possible phenotypic values fall within a desired range. In our trial simulations migration propensity did not evolve to values higher than $\eta \sim 0.2$, and hence we scale the range of values phenotypes can take between 0 and 0.25. This gives a step size of ~ 0.008 . Mutations occur with constant probability 0.001 independently in each locus. Thus mutations have small phenotypic effects and mutational steps are small. Note that one phenotype may be coded by many genotypes.

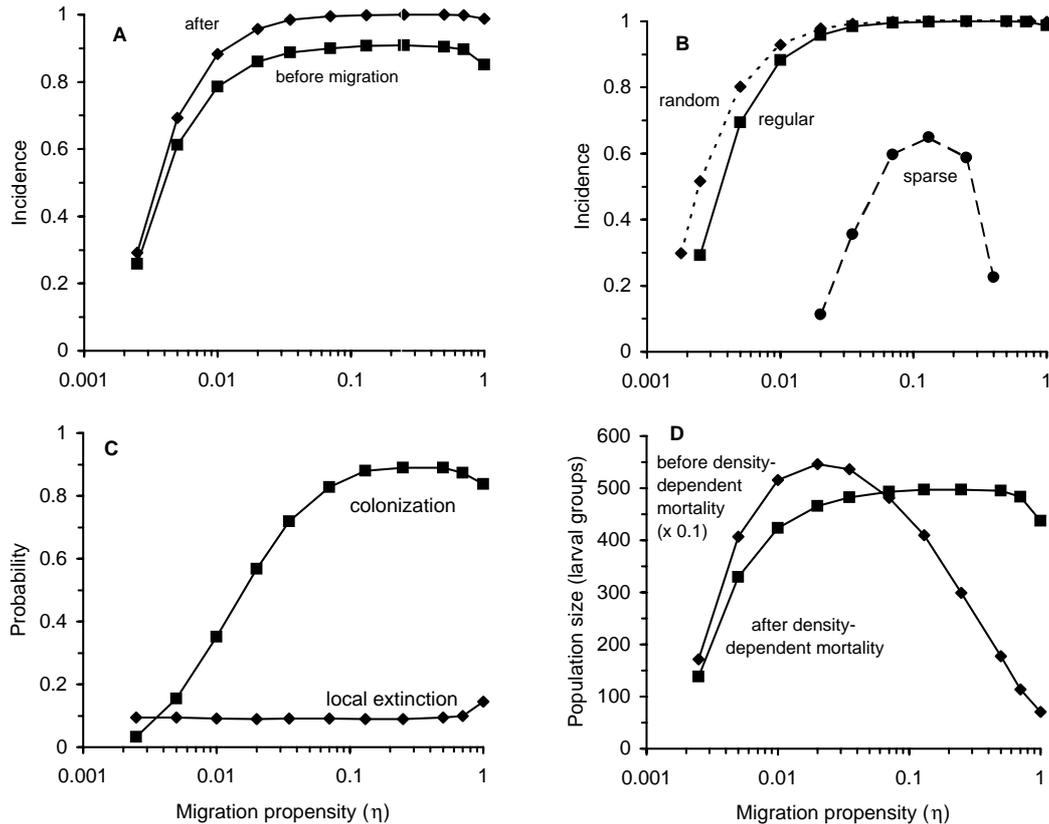


Figure 1: Dynamics and migration propensity in a hypothetical landscape (100 patches of unit area in a regular square lattice). Incidence is maximal after the migration phase in summer (upper line in A) and decreases thereafter to reach the minimum in the spring (lower line). Randomizing patch locations has no major influence on incidence, but increasing patch distances by 50% lowers incidence dramatically (B). Local extinction risk is almost independent of migration rate, but colonization probability increases with increasing migration propensity (C). Total metapopulation size after density dependence is primarily determined by incidence (D). Parameter values are given in Table 1.

Results

Migration propensity and dynamics in simple landscapes

We first examine the dependence of population dynamics on the model parameters. To avoid possible complications arising from complex spatial structures of real metapopulations and to facilitate comparisons with previous models, we use a hypothetical landscape of 100 identical patches on a 10×10 square lattice. The distance between adjacent patches is 500 m, and each patch has a carrying capacity $K = 5$ and an area $A = 1$. The daily emigration probability thus equals migration propensity (eqn. 1). Using the parameter values for the checkerspot butterflies as described in the previous section (Table 1), this landscape is well-connected and supports a viable metapopulation. The results are based on simulations of 1100 generations, with the first 100 generations omitted to eliminate transient dynamics. Simulations were initialized with all patches occupied unless otherwise stated.

The influence of migration propensity on the dynamics is summarized in Figure 1.

A very low level of migration is sufficient to maintain a viable metapopulation: risk of metapopulation extinction is negligible for migration propensities $\eta > 0.0025$. For higher levels of migration, incidence (the fraction of occupied patches) first increases rapidly, then reaches a plateau: for $\eta > 0.02$, the incidence in the spring, before migration, is ca 0.9, whereas following migration almost all patches are occupied (Figure 1A). There is thus no optimal migration propensity that would maximize the incidence. If individuals always migrate, incidence decreases slightly because of increased local extinction risk and the mortality cost of migration.

Colonization probability, which is here defined as the probability that a patch which is empty in the spring is occupied following the migration period, increases steadily with η (Figure 1C). In contrast, local extinction risk, defined as the probability that a patch occupied in the spring goes extinct before the following spring, is hardly influenced at all by migration. There are two main reasons for the latter result. First, although roughly half of the emigrants die during migration, emigration is partly compensated for by immigration (the rescue effect). Second, even a fairly high emigration rate has no significant effect on the local population sizes after density dependence, because fecundity is so high that local population sizes tend to be well above the carrying capacity before the operation of density dependence. For the same reason, total metapopulation size after density dependence is mainly determined by patch occupancy (Figure 1D). The total metapopulation size before density dependence is greatly influenced by losses during migration, and the metapopulation size peaks at a low migration propensity ($\eta \sim 0.02$).

No real metapopulation exists on a regular square lattice. This assumption, however, is not critical for the dynamics, which hardly change when the patch locations are randomized. The main difference is that in a landscape with random patch locations patch occupancy is slightly higher than with regular spacing of patches, and the metapopulation is viable for slightly lower migration propensity (stippled line in Figure 1B). This effect occurs because randomization of patch locations introduces some clustering of patches, increases average connectivity among patches, and thereby results in more efficient colonization of empty patches (Adler and Nuernberger 1994, Hanski and Ovaskainen 2000).

The dynamics are sensitive to changes in inter-patch distances. We introduce another landscape by increasing the distances between the patches by 50% (increasing the value of the scaling parameter α would have exactly the same effect). This landscape will be referred to as 'sparse'. Dynamics in the sparse landscape are more sensitive to changes in migration propensity (dashed line in Figure 1B) than in the original 'dense' landscape, and now certain level of migration maximizes incidence. Colonization of empty patches is now more difficult than in the dense landscape due to high migration mortality (only $\sim 5\%$ of migrants survive). Indeed, too much migration leads to the extinction of the entire metapopulation (Figure 1B), as has been observed in general metapopulation models (Hanski and Zhang 1993).

Evolution of migration in simple landscapes

Figure 2 illustrates the evolution of migration propensity in the landscape introduced in the previous section. The simulations were initiated with monomorphic populations with either high ($\eta = 0.21$, Figure 2A) or very low ($\eta = 0.015$, Figure 2B) migration propensity. In both cases, the sequence of events is similar. First, the population becomes polymorphic as mutations introduce new phenotypes. Strong directional selection favors phenotypes with intermediate migration propensities, and the population average changes. After about 500 generations, the metapopulation has evolved to the average migration propensity of ~ 0.1 . Thereafter, both the average and the variance of the phenotypic distribution

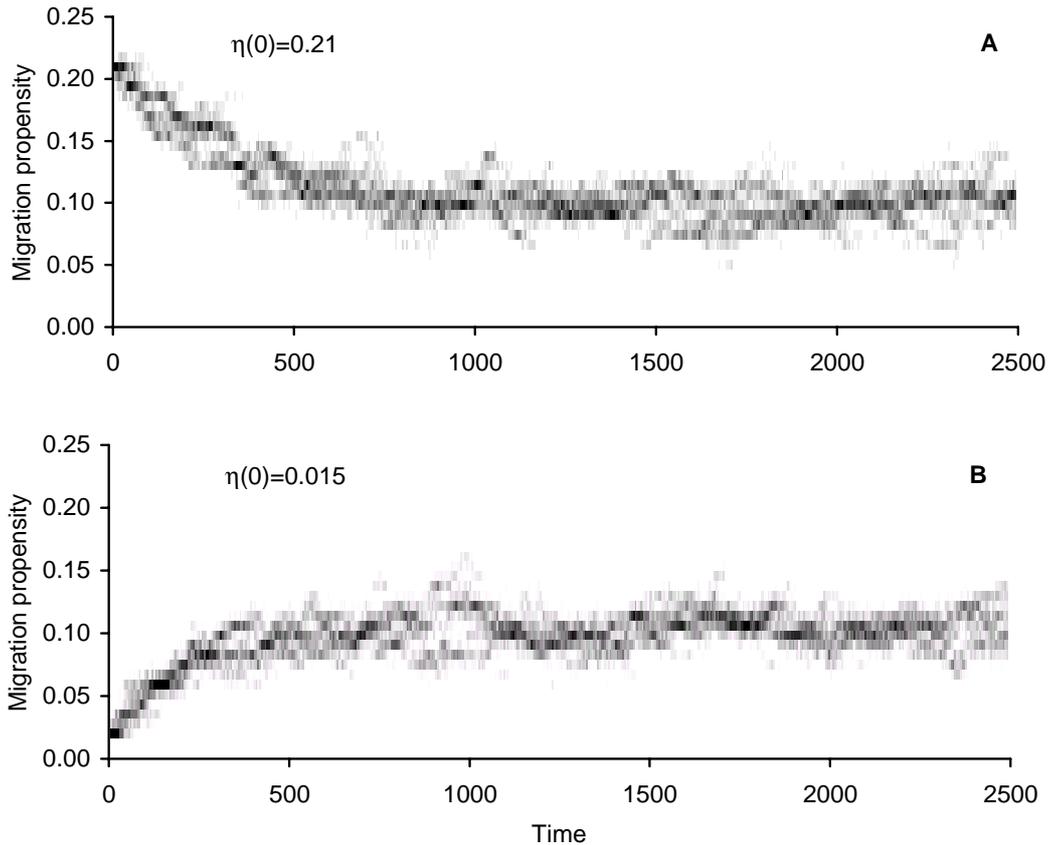


Figure 2: Evolution of phenotypic distributions of migration propensity. After about 500 generations, the long-term mean of the distribution has converged to a similar value, regardless of the initial strategy (A: $\eta(0) = 0.21$, B: $\eta(0) = 0.015$). Shading indicates the abundances of the phenotypes. Parameter values are given in Table 1.

fluctuate, but there are no long-term trends: the metapopulation has attained a quasi-stationary phenotypic distribution. We term the long-term average of this distribution as the evolutionarily optimal migration propensity. Note that this migration propensity is not optimal in the sense that it would maximize metapopulation size; rather, it is optimal in the sense that it is an approximation of an evolutionarily stable strategy (ESS). In all the subsequent simulations, optimal migration propensity and other statistics were calculated on the basis of at least five replicate simulations of 1500 generations from which the first 500 generations were omitted.

We next study the influence of the model parameters on the evolutionarily optimal migration propensity. We first focus on the distance dependence of migration, as determined by the parameter α . Increasing α increases the effective distances between the patches, and thereby leads to higher mortality and shorter average migration distances. The average migration distance is approximately given by $1/\alpha$.

Distance dependence of migration has a strong influence on optimal migration propensity (Figure 3A). When distance dependence is weak ($\alpha = 0-2$), migration propensity evolves to a relatively high level. Increasing distance dependence selects for decreased migration. However, this trend is reversed when distance dependence becomes strong ($\alpha \sim 6$ or higher). For very strong distance dependence, the metapopulation is no more viable.

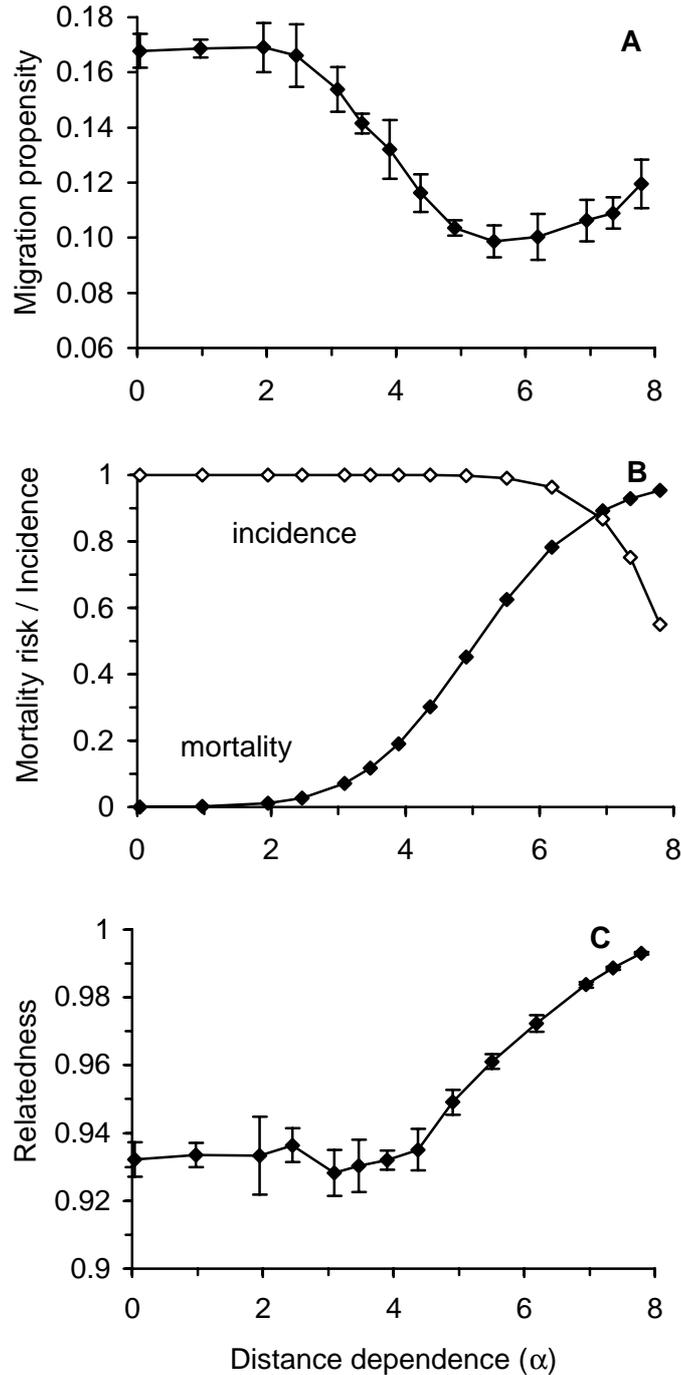


Figure 3: Evolutionarily optimal migration propensity has U-shaped dependence on distance dependence of migration, parameter α . (A). Vertical bars give the standard deviation from results of five replicates. If distance dependence is low, isolation does not much hinder migration, and average migration distance is large. For strong distance dependence, migration is confined to the nearest neighbors, and for even larger values of α an extinction threshold is reached. Increasing distance dependence results in higher mortality during migration, which in turn decreases colonization rate and incidence (B). Average within-patch relatedness, calculated as the proportion of shared loci, increases with distance dependence (C). Parameter values are given in Table 1.

At least three different selective forces seem to be responsible for the non-monotonic dependence of optimal migration propensity on the parameter α . The decline in migration propensity with increasing α is primarily driven by increasing migration mortality (Figure 3B). However, increasing distance dependence decreases connectivity in the metapopulation, and above a certain level average within-patch relatedness of individuals starts to increase (Figure 3C) and the incidence starts to decrease (Figure 3B). These changes create a selection pressure for increased migration because of increasingly severe kin competition and because of higher pay-off for successful immigrants through weak or absent competition in the newly-colonized patches. The relative strengths of the latter two selective forces will be examined later.

Similar non-monotonic pattern is obtained when migration mortality (λ) is varied: migration propensity is high when the mortality cost of migration is very low, whereas when the cost is increased, migration propensity decreases (Figure 4A). However, for sufficiently high cost, there is again a marked increase in the optimal migration propensity. This pattern is associated with similar changes in incidence (Figure 4B) and relatedness (Figure 4C) as in the example involving α . A qualitatively similar result emerged when we made space implicit (by assuming that all inter-patch distances are equal, $\alpha = 0$) rather than explicit.

The sparse landscape incurs an additional mortality cost because of longer distances between patches. In this case, the increasing relationship between migration mortality and the optimal migration propensity dominates the full range of λ values. Close to the extinction threshold the sparse landscape selects for much higher migration propensity than the dense one for the same value of λ (Figure 4).

Migration propensity decreases monotonically with increasing local carrying capacity (Figure 5A). This decrease can be explained by two mechanisms. First, local extinction risk decreases with increasing carrying capacity, hence there is a diminishing probability that an immigrant will arrive at an empty patch, while mortality during migration is unaffected (Figure 5B). Second, there is a monotonic decrease in relatedness with increasing carrying capacity (Figure 5C).

The dependence of the evolutionarily optimal migration propensity on the carrying capacity is very similar in both dense and sparse landscapes, in spite of much higher mortality cost of migrating in the latter one. A likely explanation is that counteracting selective forces are roughly balanced: higher migration mortality selects for a decrease, whereas lower incidence and higher relatedness select for an increase in migration propensity.

Increasing average larval group size leads to only minor changes in local extinction risk and relatedness, and there is only a marginal decrease in the migration propensity. However, if larval groups are very small, local populations reach saturation less rapidly and especially newly-colonized patches become more prone to extinction. The increased extinction risk favors an increase of migration propensity from $\eta \sim 0.103$ (larval group size 12) to $\eta \sim 0.116$ when larval group size is three. The increase in migration rate takes place despite a marked decrease in average relatedness within a patch, from ~ 0.95 to ~ 0.90 , when larval group size is decreased from 12 to three. In this case, it is apparent that the selective pressure on migration rate imposed by kin selection is weak in comparison with the selective pressure caused by spatio-temporal variation in fitness.

Migration and habitat change

The above examples can all be interpreted in terms of habitat change. Increase in distance dependence (Figure 3) or migration mortality (Figure 4) are likely to occur when the quality of the matrix habitat deteriorates. Destruction of some habitat patches would

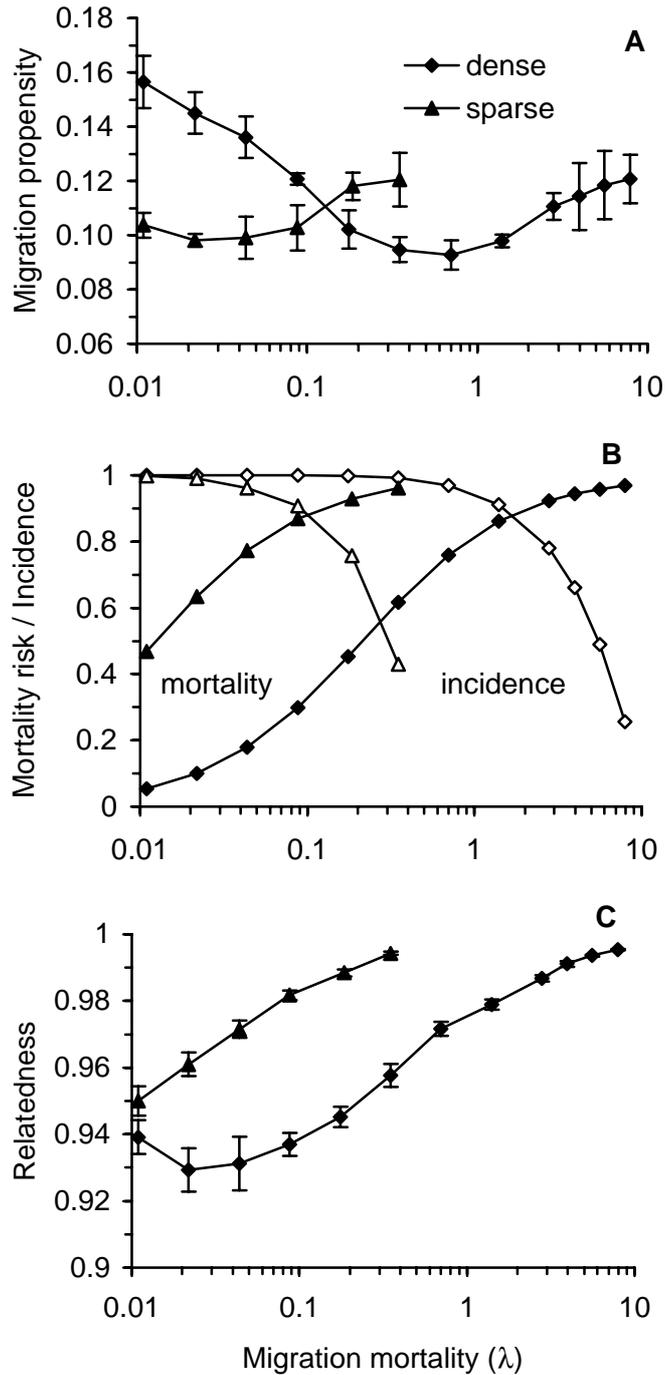


Figure 4: Evolutionarily optimal migration propensity in dense (diamonds) and sparse (distances increased by 50%; boxes) networks for different values of migration mortality (λ) (A). When mortality is very high, incidence declines to a low level (B). Metapopulation extinction will occur if migration mortality is very high. Average within-patch relatedness mostly increases with migration mortality (C). Other details as in Figure 3.

also increase migration mortality. The evolutionary response to such changes may be non-monotonic, first a decrease, but eventually, when the extinction threshold is approached, an increase in migration propensity. Decrease in patch quality is likely to be manifested as

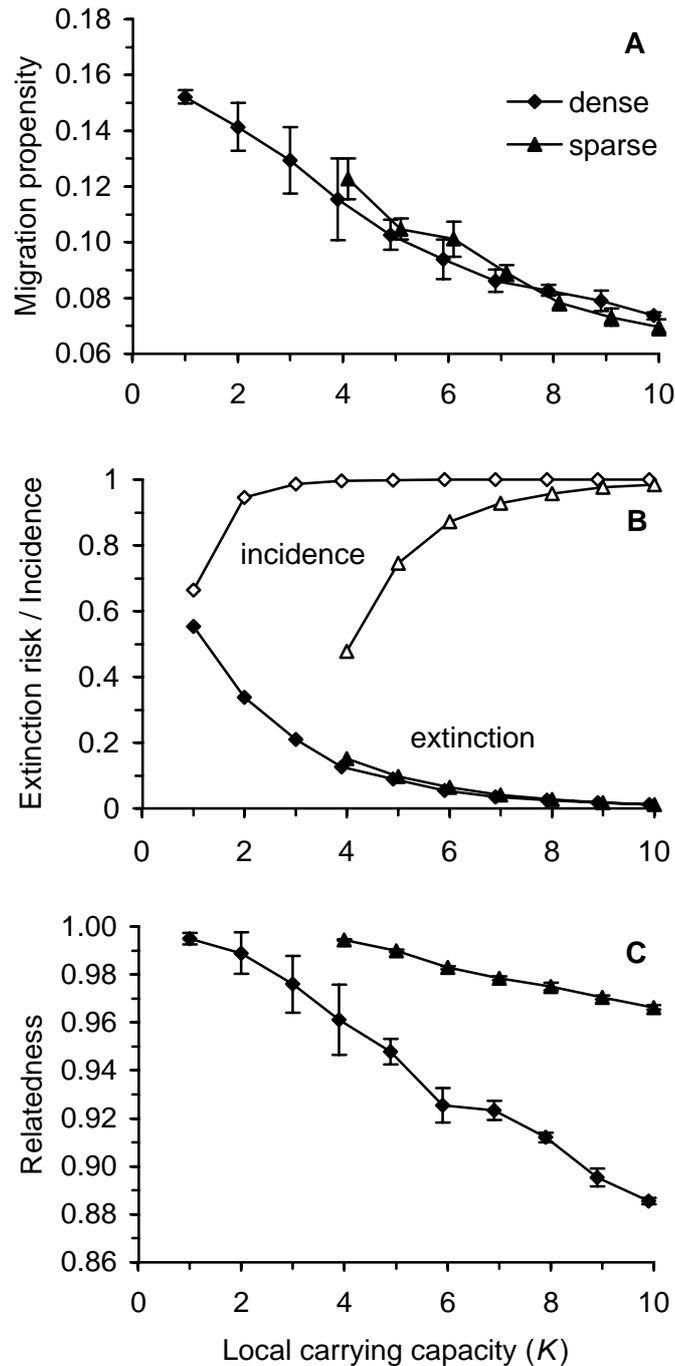


Figure 5: Influence of the carrying capacity on evolutionarily optimal migration propensity (A). Emigration rate is typically higher in sparse (boxes) than in dense landscapes (diamonds). When the carrying capacity is very small, extinction risk is high and incidence is low (B; shown only for the dense network). Curves start from the lowest carrying capacity supporting a viable metapopulation. Other details as in Figure 3.

a decrease in family size or the carrying capacity (Figure 5). Such habitat changes would favor an increase in migration propensity.

A particular example of habitat quality deterioration is given in Figure 6. In this

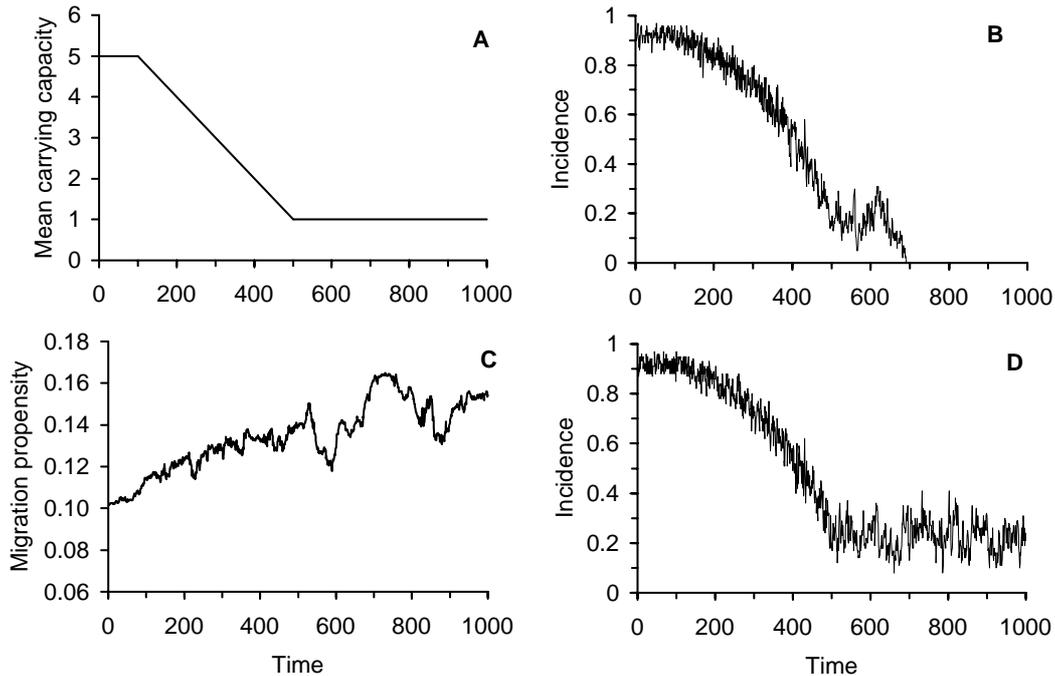


Figure 6: Evolutionary rescue in a metapopulation in a changing landscape. Habitat quality deteriorates between years 100 and 500: the carrying capacity decreases from five to one (A). If there is no evolution in the metapopulation, the habitat change leads to extinction (B). However, decrease in the carrying capacity favors an increase of migration propensity (C), and an evolving metapopulation can persist, albeit at a low level of incidence (D). Both migration propensity and incidence fluctuate strongly in the deteriorated landscape because of very small local population sizes.

example, the original landscape is our dense landscape of 100 patches, each with a carrying capacity $K = 5$. We assume that during the years 100–500, carrying capacity in one patch is decreased by one unit in each year. By the year 500, all patches have unit carrying capacities (Figure 6A). If migration propensity is fixed to the value that is optimal in the original landscape ($\eta \sim 0.1$), the metapopulation is not viable at time 500 (Figure 6B). However, if migration propensity is allowed to evolve, deteriorating habitat quality selects for increasing migration propensity, and the metapopulation is able to persist in the new landscape, although with a low incidence (Figure 6C–D). In this example evolution is able to rescue the metapopulation from extinction. Of course, whether or not such a rescue is likely to happen depends on the time scale of environmental change relative to the rate at which the metapopulation responds to selection.

Dynamics and evolution of checkerspot butterflies in real habitat networks

In this section we move on to analyze the evolution of migration rate in real highly fragmented landscapes. A strength of the present modeling approach is that it can be applied equally well to such irregular patch networks as to regular networks on lattice. We first focus on the patch network inhabited by *Melitaea diamina* in the Tampere region of Finland, consisting of 94 patches within an area of $21 \text{ km} \times 29 \text{ km}$ (Wahlberg et al. 1996).

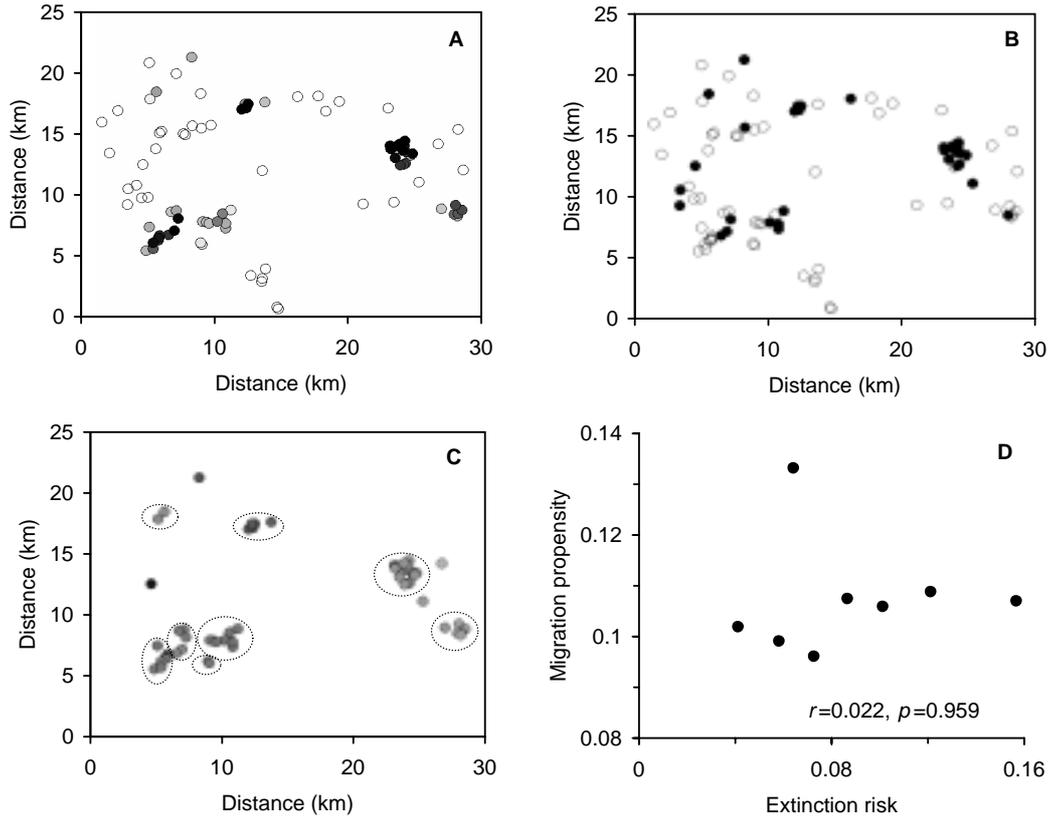


Figure 7: The predicted (A) and the observed (B, from Wahlberg et al. 1996) patterns of patch occupancy in the *Melitaea diamina* metapopulation. Shading of the dots indicates the incidence, from 0 (white) to 1 (black). In panel C, medium gray corresponds to $\eta = 0.07$ and black to $\eta = 0.14$. Regional differences in migration propensity emerge (C). Average migration propensity within a patch cluster (the clusters used in the analysis are encircled in panel C) is not correlated with average extinction risk in the cluster (D). In calculating within-cluster averages, patches were weighted with their carrying capacity. Delineation of clusters is based on the matrix ψ (eqn. 4); isolated single patches or clusters with very low incidence are ignored. Ten replicate simulations were used.

Simulations were initialized with the observed pattern of patch occupancy (Wahlberg et al. 1996). The pattern of patch occupancy predicted by the model (Figure 7A) is very similar to the observed pattern (Figure 7B, from Wahlberg et al. 1996). Dense clusters of habitat patches support assemblages of viable local populations, and the incidence is high in these clusters because of efficient recolonization. Isolated patches, if large enough, can remain occupied for a long period. However, once extinct, recolonization of isolated patches is very unlikely, and hence their incidences are low.

If migration propensity is allowed to evolve, keeping all the other parameters at their empirically estimated values, migration propensity decreases from the estimated value of $\eta = 0.130$ to $\eta \sim 0.104$ (standard deviation of ten replicates 0.005). This 'evolutionarily optimal' migration propensity is still within the 95% confidence interval of the original parameter estimate (Table 1). The pattern of patch occupancy remains almost unchanged, and there is no significant change in the level of patch occupancy. Migration propensity varies between different patches from $\eta = 0.09$ to $\eta = 0.13$ (Figure 7C). Because of

Table 3: Consequences of habitat change in the metapopulation of *Melitaea diamina*, assuming either that migration propensity has the empirically estimated value ($\eta = 0.130$), the optimal value in the original landscape ($\eta = 0.104$), or that η is evolving. Habitat was changed by eradicating 20 or 40 randomly selected patches, or by decreasing the areas of randomly selected patches by 50% until the desired amount of patch area was lost, or by decreasing carrying capacities (but not areas) of randomly selected patches by 50% until the desired amount of K was lost. All values are based on ten replicates of 1100/1500 generations (fixed η /evolving η) with transients of 100/500 generations omitted.

Scenario	Occupancy (SD)			
	$\eta = 0.130$	$\eta = 0.104$	'optimal' η	η (SD)
No habitat change	0.36 (0.04)		0.36 (0.03)	0.104 (0.005)
20 patches lost	0.24 (0.04)	0.24 (0.05)	0.22 (0.04)	0.096 (0.007)
40 patches lost	0.15 (0.03)	0.16 (0.04)	0.14 (0.04)	0.098 (0.010)
20% of patch area lost	0.20 (0.04)	0.21 (0.04)	0.18 (0.03)	0.104 (0.013)
50% of patch area lost	0.19 (0.03)	0.21 (0.03)	0.18 (0.03)	0.101 (0.005)
50% of K lost	0.097 (0.023)	0.093 (0.015)	0.086 (0.015)	0.120 (0.017)

migration, patches close to each other tend to have similar values of η . There is a statistically non-significant tendency of migration propensity to be higher in patch clusters in which survival of migrants is high (Figure 7D). Average within-patch relatedness is very high (0.988, SD 0.001) because of typically small local population sizes and clustering of patches.

Loss of habitat — be it total destruction of some patches or decrease in patch areas — has only minute evolutionary consequences on the migration propensity of *M. diamina* in the real landscape (Table 3). In both cases, migration propensity tends to decrease, which is accompanied by a minute decrease in average patch occupancy. However, if only patch quality (K) deteriorates, but patch areas stay the same, such that movement patterns between the patches remain unchanged, there is an increase in migration propensity (Table 3).

We next use the model to study evolution of migration rate in the related species *Melitaea cinxia* in the Åland Islands in southwest Finland. The two *Melitaea* species share the same basic biology, to the extent that parameter values of the IFM estimated from *M. cinxia* (Hanski et al. 1996) predicted well the distribution of *M. diamina* in its own habitat patch network (Wahlberg et al. 1996). We analyze two patch networks of *M. cinxia*, of which the first one is a relatively sparse one with 183 patches in a triangular area of 23 km high and 29 km wide. The second network consists of 272 patches within an area of 12 km \times 14 km. As a consequence of the higher patch density in this second network, probability of surviving migration is 54%, as compared to 44% in the sparse network. Average patch size is similar in both networks, 0.22 ha in the dense network and 0.23 ha in the sparse one.

Migration propensity evolves to a higher level in the sparse network ($\eta = 0.118$, SD 0.006) than in the dense one ($\eta = 0.104$, SD 0.006). The western half of the sparse network is so sparse that all local populations go extinct (Figure 8). Because of clustering of the patches, the rest of the network is fairly dense at the regional (within-cluster) scale, and the probability of successful migration among the patches that were occupied after the transient was 51% in the sparse network and 55% in the dense one.

Clustering of patches in the sparse network allows regional differences in migration propensity to evolve (Figure 8A), whereas the dense network remains more homogeneous

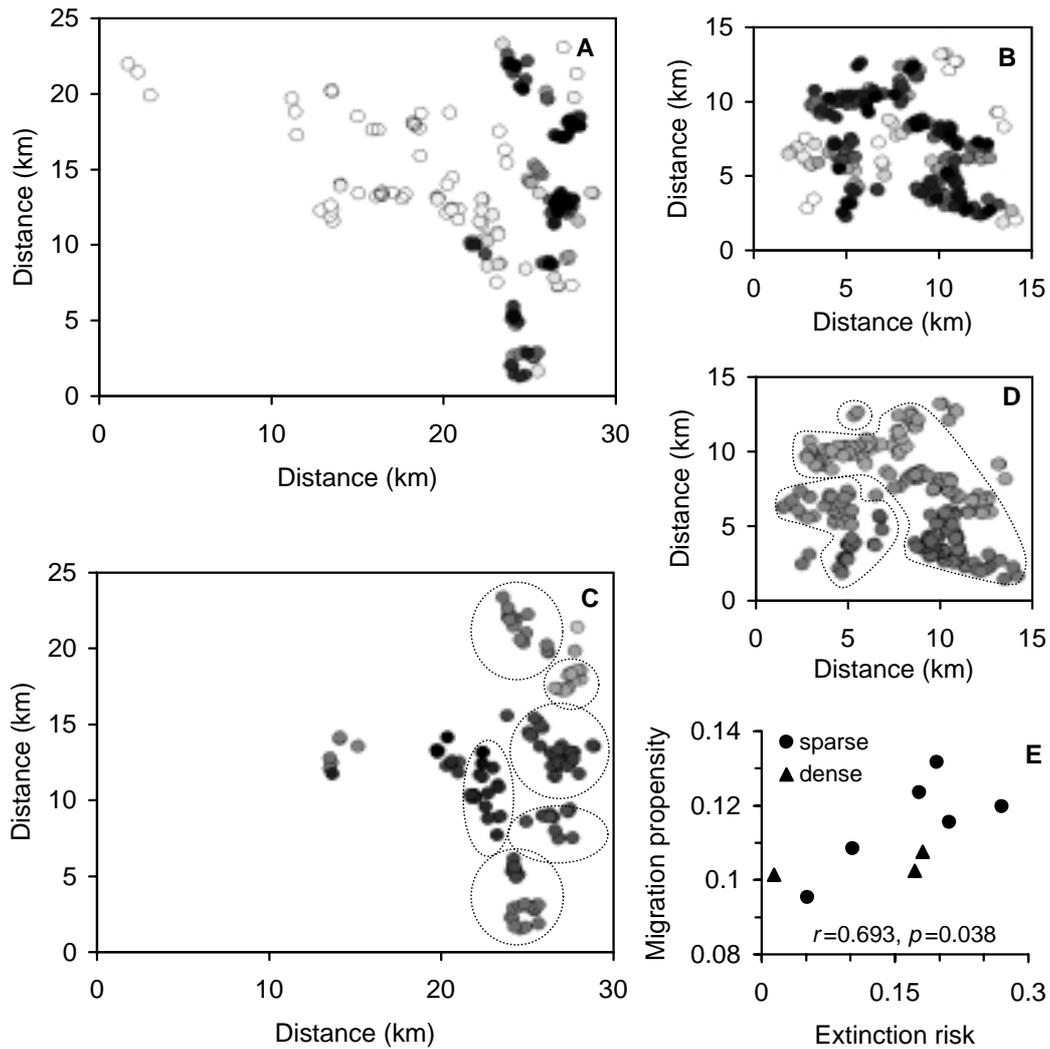


Figure 8: Predicted patch occupancy (A, B) and migration propensity (C, D) in two contrasting large habitat patch networks inhabited by *Melitaea cinxia* in the Åland Islands. The network in panel A is sparse; only the eastern part of the network supports a viable metapopulation. Clustering of the patches allows some regional differences in migration propensity to evolve (C). The other network (B) is dense and less clustered. Migration propensity is fairly homogeneous over the network (D). Within-cluster average migration propensity is correlated with average extinction risk (E). Other details as in Figure 7.

(Figure 8D). Differences in the local extinction risk between different patch clusters are large, and the migration propensity is positively correlated with extinction risk (Figure 8E). Combining data from the two *Melitaea* species (Figures 7D and 8E), there is a significant positive correlation ($r = 0.506$) between extinction risk and migration propensity. Average within-patch relatedness is very high in both networks, 0.990 (SD 0.001) in the sparse one and 0.985 (SD 0.001) in the dense one.

Discussion

The model described and analyzed in this paper is an individual-based simulation model. Such models have well-known shortcomings, of which the most obvious one is lack of generality — no exhaustive model analysis is possible. This drawback must be balanced against potential advantages. Provided that sufficient empirical information is available to justify model assumptions and to estimate parameter values, a carefully constructed simulation model can be tailored for particular systems to investigate, in a realistic manner, biologically significant questions. We consider that this approach is warranted in the present case. First, we can employ two well-parameterized submodels to construct a large part of the present model and to obtain empirical estimates of the parameter values (summarized in Table 1). Second, the existing extensive knowledge about butterfly metapopulations and their landscapes (Thomas and Hanski 1997) helps focus the investigation on questions that have a broad significance not only for butterflies but for a large number of other taxa with similarly structured metapopulations (Hanski 1998, 1999). And third, the model can be used to make testable predictions.

The number of model parameters is relatively large, 15 (Table 1), but most of them can be estimated rigorously with empirical data. Structural assumptions about adult movement behavior and extinction-colonization dynamics are also well supported by empirical data. We therefore consider that our results are fairly robust and representative for the types of systems exemplified by the butterfly metapopulations. For the well-studied *Melitaea diamina* metapopulation, the model predicted an optimal migration propensity ($\eta = 0.104$, standard deviation 0.006) that is not significantly different from the empirically estimated value (0.130, 95% confidence limits 0.103 and 0.176; Table 1). Though this is not a critical test of the model structure nor of the optimality of the observed migration rate, the match between the observed and predicted values is encouraging.

Another shortcoming of individual-based models is that it is often difficult to know why a certain result is obtained. Of the processes that potentially influence the evolution of migration rate (Johnson and Gaines 1990, Olivieri and Gouyon 1997) some are included in our model whereas others are not. The key processes explicitly included are spatial and temporal variation in population density, including the extinction and re-establishment of local populations, resource and kin competition, and the direct cost of migration (elevated mortality during migration). Factors not included are inbreeding avoidance and anything else related to sexual reproduction, as well as any more complex behaviors leading to conditional migration, for instance density-dependent emigration and immigration. Though these latter processes have some significance in many species, including the checkerspot butterflies studied here (Kuussaari et al. 1996, 1998, Saccheri et al. 1998), we consider that spatio-temporal variation in fitness due to stochastic population dynamics, mortality during migration and kin competition are the primary determinants of the evolution of migration rate in many insect metapopulations, and hence the present model represents a realistic base-line model.

Many of our evolutionary results can be explained both by selection associated with extinction-colonization dynamics and by kin selection arising from avoidance of kin competition. For example, positive relationship between carrying capacity and migration rate can be explained both by changes in kin competition (Frank 1986, Taylor 1988, Gandon 1999, Gandon and Michalakis 1999) and by changes in extinction risk. However, in some cases these selective forces have opposing directions, allowing an assessment of which one is stronger in that specific case. Increasing mortality cost of migration up to moderate levels apparently selected for decreased migration rate, despite increasing relatedness (Figures 3 and 4). Similarly, reduced larval group size increased local extinction risk which ap-

parently increased migration rate, despite decreased relatedness associated with reduced larval group size. Thus, selection driven by extinction-colonization dynamics was clearly stronger than kin selection in these cases. This result is not due to lack of kin selection in our model, as can be shown by the following example.

The operation of kin selection can be shown by artificially decreasing average relatedness of individuals in a manner that leaves extinction-colonization dynamics untouched. To achieve this, we ran five replicate simulations of the dense landscape, with an additional procedure of randomly mixing all the larval groups among populations before emergence of adults in the spring, without changing local population sizes. Such mixing caused a clear decrease in relatedness, from 0.949 (SD 0.010) to 0.927 (0.011), and a correlated response in the evolutionary optimal migration propensity, from 0.104 (0.003) to 0.088 (0.008).

The assumption of asexual reproduction casts some doubt to our results regarding kin selection. However, checkerspot butterflies mate only once and generally before migration, and hence the relatedness within a larval group is likely to be high. Therefore asexuality is unlikely to be a critical assumption in our model.

Many previous studies of the evolution of migration rate in metapopulations have focused on the consequences of local extinction rate on the optimal migration propensity. For some time the consensus has been that the optimal migration propensity increases with extinction rate (van Valen 1971, Comins et al. 1980, Levin et al. 1984). Recently, Ronce et al. (2000a) and Parvinen et al. (2000) have challenged this conclusion and suggested that the relationship is non-monotonic, with very high extinction rate leading to reduced migration propensity. Unlike the previous authors, Ronce et al. (2000a) and Parvinen et al. (2000) have studied structured metapopulation models, with an explicit description of local dynamics. High extinction rate shifts the distribution of local population sizes towards smaller populations (Hanski and Gyllenberg 1993), in which resource competition is weak and contributes little to selection for emigration (Ronce et al. 2000a). On the other hand, if a large fraction of patches remain uncolonized because of low numbers of potential immigrants, expected fitness of an emigrant may be increased. The latter effect can occur in the model of Parvinen et al. (2000) but not in the model of Ronce et al. (2000a).

In our model, local extinction is a mechanistic consequence of habitat patch size and stochastic local dynamics, which we have parameterized using empirical data. The combined data for both *Melitaea* species reveals a monotonically increasing relationship between migration propensity and extinction risk. The same relationship holds for *M. cinxia* alone (Figure 8E), but not for *M. diamina* (Figure 7D). Lack of relationship between extinction risk and η in *M. diamina* is probably due to rather small differences among the clusters, too small for a significant relationship to emerge. In contrast, there are large differences in extinction risk between the clusters of patches in the metapopulations of *M. cinxia* (Figure 8E).

To facilitate further comparison with the models of Ronce et al. (2000a) and Parvinen et al. (2000), we increased local stochasticity in our model using the hypothetical dense landscape. We first increased variance in over-wintering survival and/or family size. The resulting increase in local extinction risk selected for a monotonic increase in migration rate. The increase in extinction risk introduced in this manner was not sufficient to cause a significant decrease in incidence nor in local population sizes after density dependence — the variances of diapause survival and family size are bounded if the means are kept unchanged. However, if we make a structural change to our model by introducing exogenous extinctions, a non-monotonic relationship emerges in our model (Figure 9). However, the eventual decrease in migration propensity occurs only close to the extinction thresh-

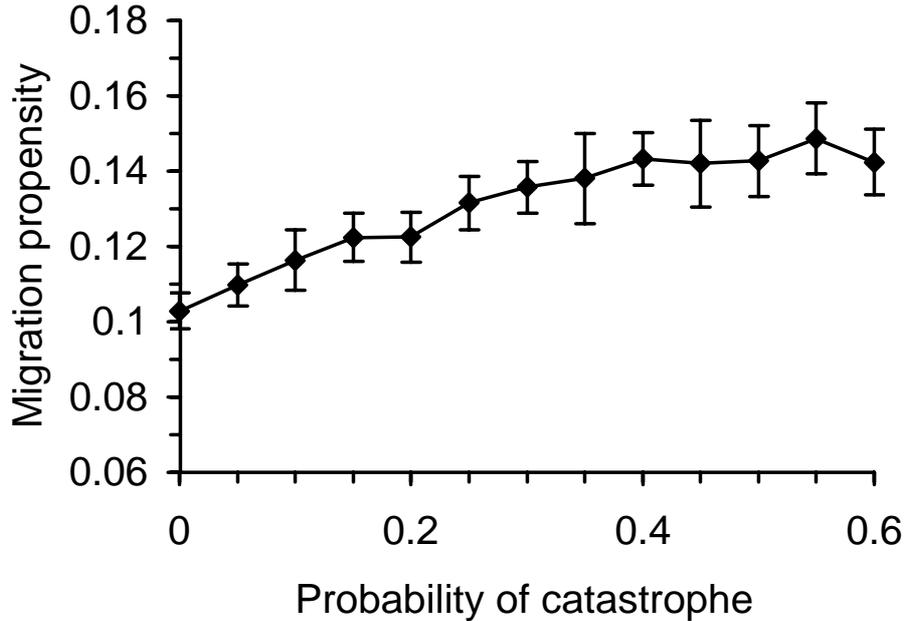


Figure 9: Influence of local catastrophes on the evolution of migration propensity. Catastrophes occur in summer after the migration period and destroy all the larvae in a habitat patch. Probability of catastrophe greater than ~ 0.6 leads to metapopulation extinction. The results are mean values of ten (probability of catastrophe less than 0.4) or twenty replicates (otherwise) with standard deviations indicated by vertical bars. Other parameters as in Table 1.

old, when the annual probability of catastrophic extinction is very high, in the range 0.55–0.6. Frequent local catastrophes leave population densities in the occupied patches unsaturated, which favors decreased emigration despite the large fraction of empty patches available for colonization. This effect becomes more pronounced for smaller larval group sizes. Note that the predicted decrease in migration rate close to the extinction threshold is moderate, far from the dramatic decline in the model of Ronce et al. (2000a). We suggest that the strong negative relationship found by Ronce et al. (2000a) is due to questionable simplifying assumptions of their model.

One biologically interesting question in the context of the present model relates to the consequences of environmental change on migration rate. Several kinds of environmental changes can be considered with the present model, including a change in the number and areas of existing habitat patches, change in the quality of the patches (the carrying capacity, K), and change in the quality of the matrix habitat. Decreasing patch areas increase extinction rate (as K decreases), whereas increasing patch isolation and reduced quality of the matrix habitat increase migration mortality. Note that our model assumes an ability to distinguish between habitable patches and the uninhabitable matrix habitat, in contrast to models of diffusive dispersal analyzed by Travis and Dytham (1998, 1999).

We find it helpful to consider selection on migration propensity at two levels, at the level of local populations and at the level of the entire metapopulation, where the entities are local populations (though one can also interpret all selection pressures at the individual level). At the local and individual levels, increased migration is selected for by resource and kin competition and by reduced migration mortality. At the metapopulation level, finite lifetime of local populations guarantees the presence of empty patches which can

only be colonized by migrating individuals. Selection for increased migration rate at the metapopulation level is limited by population turnover. The opposing selection pressures lead to a non-monotonic change in the optimal migration rate with environmental deterioration. Initially, when the metapopulation occupies most of the habitat, selection for reduced migration rate due to increasing migration mortality dominates, but eventually, when the landscape has deteriorated to a point where many patches remain empty, migration rate tends to increase. The non-monotonic change has been predicted previously by Comins et al. (1980). Gandon and Michalakis (1999) demonstrate a similar effect based on competition among kin in a spatially implicit model. Our analyses show that although kin competition is present in our model and influences the optimal migration rate, in quantitative terms selection due to spatio-temporal variation in fitness is the dominant process.

Our results demonstrate how, in principle, an evolutionary change in migration rate can rescue a metapopulation from extinction in a deteriorating landscape (Figure 6). Whether or not evolutionary rescue is really important depends on the rate of environmental change in relation to the adaptive potential in the species (Lynch and Lande 1993, Gomulkiewicz and Holt 1995). The adaptive potential depends on population size and on genetic variance in the adaptive trait. In our model, the landscape structure largely determines the spatially structured population size, while the genetic variance is a function of the mutation rate and the genetic architecture of the trait. Unfortunately, as the mutation rate and genetic architecture are unknown, we cannot quantitatively assess the potential for evolutionary rescue. Our results lend limited support to both viewpoints — that evolutionary rescue is, and is not, of practical significance.

The good news for evolutionary rescue include the observation that, according to the present model, considerable variation in migration propensity can be maintained in metapopulations due to weak phenotypic selection close to the evolutionary optimum (Figure 2). Furthermore, predictions for real butterfly metapopulations demonstrate considerable variation in the optimal migration propensity in different parts of single patch networks, further adding to the variance in the trait value at the metapopulation level and demonstrating the potential for evolution in response to habitat change. Travis and Dytham (1999), analyzing another individual-based simulation model, also found regional adaptation in the migration rate, though in their lattice model with nearest-neighbor migration, differentiation occurred just between marginal and central 'populations' living within a large expanse of suitable habitat (edge 'populations' suffering from migration mortality). Some empirical studies have claimed to have found evidence for regional adaptation in migration rate in response to landscape structure (Thomas et al. 1998), but the evidence is not very conclusive. Note that the present model can be used to make testable predictions about regional variation in migration rate in real landscapes (see Figures 7 and 8) and it may thereby play a useful role in further studies of regional adaptation in migration rate.

Turning to the bad news, the predictions summarized in Table 3 for various scenarios of change in a real landscape in which up to half of the pooled habitat was lost should temper our expectations about the potential significance of evolutionary rescue. In these examples, migration propensity indeed increased in the scenario with the greatest habitat loss, but the increase in optimal migration propensity was only moderate (from $\eta = 0.104$ to 0.12) and, most importantly, the consequences for metapopulation size were minimal, with the fraction of occupied patches being 0.09–0.1 for the relevant range of migration propensities. Such a tiny difference is likely to be completely swamped by additional stochastic effects in real environments. This example suggests that evolutionary rescue

may have significant metapopulation dynamic consequences only in special circumstances. It should also be remembered that evolutionary change can be detrimental for a population. This might happen if local selection gradient favors a decrease in migration rate to a low level which precludes long-term persistence, even though some higher migration rate would allow persistence. However, we have not observed this possibility in our model.

Our spatially realistic individual-based metapopulation model complements existing simpler and more general models in two respects. First, it yields predictions which are directly applicable to real metapopulations. Some of these predictions can be tested, whereas others provide insight to management and conservation of real metapopulations. Second, the present model helps evaluate the robustness of the predictions of simpler models, which necessarily make many unrealistic assumptions. It is encouraging that our results are consistent with the conclusions based on the earlier models, suggesting that many gross simplifications of analytical models do not matter that much. At the same time, we have been able to assess in quantitative terms the likely contribution of particular processes to the evolution of migration rate, such as kin competition. Our overall conclusion is that the dominant force driving the evolution of migration rate in the kind of metapopulations considered here is spatio-temporal variation in fitness due to stochastic population dynamics.

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