

**Interim Report**

**IR-00-035**

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**Evolution of Dispersal in Metapopulations  
with Local Density Dependence  
and Demographic Stochasticity**

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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.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

These and many more problems possess a common source: the interactions of individuals are bound to change the environments these individuals live in. By closing the feedback loop in the evolutionary explanation, a new mathematical theory of the evolution of complex adaptive systems arises. It is this general theoretical option that lies at the core of the emerging field of adaptive dynamics. In consequence a major promise of adaptive dynamics studies is to elucidate the long-term effects of the interactions between ecological and evolutionary processes.

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## Abstract

Selective pressures governing the evolution of dispersal rates are difficult to evaluate and currently poorly understood. In particular, predictions of evolutionarily stable dispersal strategies have only been derived under a number of limiting conditions regarding the ecology of dispersing species. In this paper we predict the outcome of dispersal evolution in metapopulations based on a suit of assumptions that are more likely to be met in the field: (i) population dynamics within patches are density-regulated by realistic growth functions, (ii) demographic stochasticity resulting from finite population sizes within patches is accounted for, and (iii) the transition of individuals between patches is explicitly modelled by a disperser pool. In addition we make few further changes which add to the models interest for comparison purposes; (iv) individuals can disperse between habitable patches throughout their lifetime, and (v) metapopulations are described in continuous time instead of relying on season-to-season descriptions. Extending available models in regard to these features, we demonstrate the existence of two general patterns of metapopulation adaptation. We show, first, that evolutionarily stable dispersal rates do not necessarily increase with rates for the local extinction of populations due to external disturbances in habitable patches. Instead, without demographic stochasticity, adapted dispersal rates exhibit a maximum for intermediate levels of disturbance and fall off for both higher and lower rates of local extinction. Second, we describe how the demographic stochasticity that inevitably occurs in finite populations affects the evolution of dispersal rates. Contrary to predictions from deterministic models, evolutionarily stable dispersal rates in metapopulations composed of small local populations can remain high even when rates of local extinction are low. The first pattern is shown to be robust, provided that demographic stochasticity is not too severe, under a range of local growth conditions, including logistic growth and its variants. We also demonstrate that high degrees of demographic stochasticity can enrich the behavior of adapted dispersal rates in response to varied levels of disturbance: monotonic increases or decreases can be observed as well as intermediate maxima or minima.

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# Evolution of Dispersal in Metapopulations with Local Density Dependence and Demographic Stochasticity

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## 1 Introduction

Metapopulations and their dynamics have become a central subject of conservation ecology and evolutionary ecology. Accounting for the spatial fragmentation occurring in many species' habitats, the study of metapopulations is providing new insights into the impacts of spatial heterogeneity on population viability and on the evolutionary forces acting on key life-history traits.

In this context, the evolution of dispersal rates has attracted particular attention (Gandon 1999; Gandon & Michalakis 1999; Gyllenberg & Metz 1999; Metz & Gyllenberg 1999; Parvinen 1999; Ronce *et al.* 2000; Nagy *in press*; Heino & Hanski *submitted*). One reason is that changes in dispersal strategies provide an option for threatened populations to respond to the perpetual fragmentation of their habitats. Consequently, success or failure of such adaptation often determines whether a challenged population can persist. Moreover, evolution of dispersal is driven by selection pressures that are inherently more complex than those arising in well-mixed populations. In particular, adaptive features that improve a phenotype's competitiveness within patches may well have detrimental effects on the same phenotype's ability to spread between patches, and vice versa. To evaluate the evolutionary consequences of such two-level selection pressures and to assess the relative strength of their components has proven to be very difficult, with general results essentially lacking. Yet, we can be confident that the ecological details assumed at both levels of population structure can qualitatively affect evolutionary outcomes. For this reason, it is important to cast investigations of adapting dispersal rates in ecological settings that are not only amenable to analysis but, at the same time, provide a sufficiently close match with conditions in the field by epitomising their salient features.

In this paper we present and investigate an evolutionary metapopulation model that aims at incorporating more realistic ecological detail into studies of dispersal evolution. We focus on three distinct aspects that are all intended to improve the match between the modelling exercise and ecological reality.

First, most previous studies of dispersal evolution have relied either on Levins-type models (Levins 1969, 1970), which altogether ignore the within-patch dynamics of populations, or, instead, have assumed relatively simple types of local population regulation, based on a ceiling for local population sizes (Olivieri *et al.* 1995; Olivieri & Gouyon 1997;

Ronce *et al.* 2000; see also Hanski *et al.* 1996; Hanski 1998). In the latter case, populations approach the ceiling without density regulation and then abruptly stop growing once the ceiling is hit. In contrast, following recent studies on structured metapopulations (Gyllenberg & Hanski 1992,1997; Gyllenberg *et al.* 1997; Gyllenberg & Metz 1999; Metz & Gyllenberg 1999) we rest our analysis on fully density-regulated local population dynamics, as they are commonplace in studies of single populations. The consequences of logistic growth rates and of more general variants are investigated in detail.

Second, we focus on the implications of stochastic population dynamics. A central conceptual argument in our understanding of dispersal evolution is based on the notion of bet hedging. Specifically, dispersal is advantageous because growth conditions as well as the length of undisturbed periods of growth tend to differ randomly between patches. For this reason, it is essential to incorporate these two kinds of stochastic factors into models of metapopulation adaptation; in our approach, both environmental stochasticity due to local extinction and demographic stochasticity due to individual-based reproduction and mortality are considered. In the following local extinction risk means all the time risk of local extinction due to external disturbances, not demographic stochasticity.

Third, some models of metapopulation dispersal assume that individuals migrate instantaneously from one patch to another (Hastings 1983; Olivieri *et al.* 1995; Doebeli & Ruxton 1997; Olivieri & Gouyon 1997; Parvinen 1999). In real ecological systems, however, individuals in transit between patches are migrating for a certain duration before they can settle again; during this period of stochastic length they tend to experience impeded reproduction and an increased level of mortality. By introducing a disperser pool as in Gyllenberg & Hanski (1992) this mechanism is incorporated into our model; see also Giles & Goudet (1997).

In addition to these improvements we make two further changes that add to the models interest for comparison purposes: Fourth, we allow for individuals to disperse between metapopulation patches more than once during their lifetime. Such behaviour occurs in a number of animal metapopulations. This contrasts with dispersal at birth as studied for example in the context of plant metapopulations. Fifth, we allow metapopulation dynamics to unfold in continuous time such that processes of reproduction or dispersal do not have to be synchronised. This contrasts with season-to-season descriptions in discrete time, as they are employed by some existing models (Gyllenberg *et al.* 1993, 1996; Hastings 1993).

A complete description of our evolutionary metapopulation model, incorporating the different features outlined above, is provided in Section 2. In Section 3 we show that dispersal rates adapted to different risks of local extinction can exhibit an intermediate maximum. In other words, increasing levels of disturbance can lead to higher as well as lower dispersal rates. Adaptations of dispersal rates to different risks of dying during migration, on the other hand, show a monotonic trend. That demographic stochasticity strongly affects evolutionarily stable dispersal strategies is demonstrated in Section 4. The findings presented there show that deterministic models that ignore the implications of finite local populations can be qualitatively in error. In Section 5 we investigate the robustness of our results under variations in local density regulation and show that the highlighted patterns of metapopulation adaptation persist for different kinds of growth regimes.

## 2 Model description

We consider a metapopulation with  $N$  patches of habitable environment. Given a local population size of  $n$  individuals within a patch, per capita birth and death rates are given by  $b_n$  and  $d_n$ , respectively. Individuals migrate out of their patches at rate  $m$ , thus entering the disperser pool of the metapopulation. While in the disperser pool, individuals experience mortality at rate  $\tilde{d}$ . They leave the disperser pool by settling into a new patch at rate  $s$ . Extinction of a local population due to external disturbances occurs at rate  $e$ .

Within this ecological setting we investigate the adaptation of dispersal rates  $m$ . We assume that the number of patches  $N$  is large enough for the entire metapopulation not to be liable to chance extinction by demographic stochasticity; otherwise, evolutionarily stable dispersal rates obviously cannot be attained. Equations for this evolutionary metapopulation model are summarised in Appendix A. Notice that because of the individual-based nature of this model and due to the existence of external disturbances, local populations are subject to both demographic and environmental stochasticity. This implies that although patches are intrinsically equivalent, the local environments experienced by individuals typically show a broad spectrum of variation, with some patches being overcrowded while others harbouring only small populations or being completely empty.

The growth of local populations is governed by density regulation. For simplicity, we assume that per capita birth rates are unaffected by density,  $b_n = r$ , while per capita death rates increase linearly with local population size,  $d_n = rn/k$ , where  $r$  is the intrinsic growth rate of local populations and  $k$  determines the local carrying capacity of patches. Local growth consequently is logistic,  $f_n = b_n - d_n = r(1 - n/k)$ . Departures from this growth regime are investigated in Section 5.

## 3 Migration risk and extinction risk

The most important determinants for the evolution of dispersal rates are the mortality risk experienced by a migrating individual and the extinction risk to which local populations are exposed. The former can be interpreted as a cost of dispersal and is thus expected to select for lower rates of migration. On the other hand, local extinctions make it impossible for a metapopulation to persist without dispersal. This fact was already stated in Van Valen (1971). Local extinctions moreover result in empty or thinly populated patches, the existence of which makes dispersal profitable. For these reasons, increasing extinction risks are expected to select for higher dispersal rates.

We assess the validity of these heuristic predictions by systematically evaluating the evolutionarily stable dispersal rates under a range of migration and extinction risks. For this purpose we employ a modification of the model presented in the previous section by assuming that local carrying capacities are large. Two reasons motivate this consideration. First, the assumption of large local populations allows for approximating our stochastic metapopulation model by a deterministic one. This simplification is frequently employed in the literature (Doebeli & Ruxton 1997; Gandon 1999; Gandon & Michalakis 1999; Gyllenberg & Metz 1999; Parvinen 1999) and facilitates the determination of evolutionarily stable strategies. Equations for the approximate deterministic model are given in Appendix B. A second reason is that we wish to emphasize the limitations of such deterministic descriptions: by comparison, our results in Section 4 highlight the importance of demographic stochasticity and the danger of ignoring it in deterministic approximations.

Evolutionarily stable rates of migration, resulting from different risks of migration and extinction, are presented in Figure 1. In Appendix C we explain why the resulting

CSS dispersal rate and population size at CSS

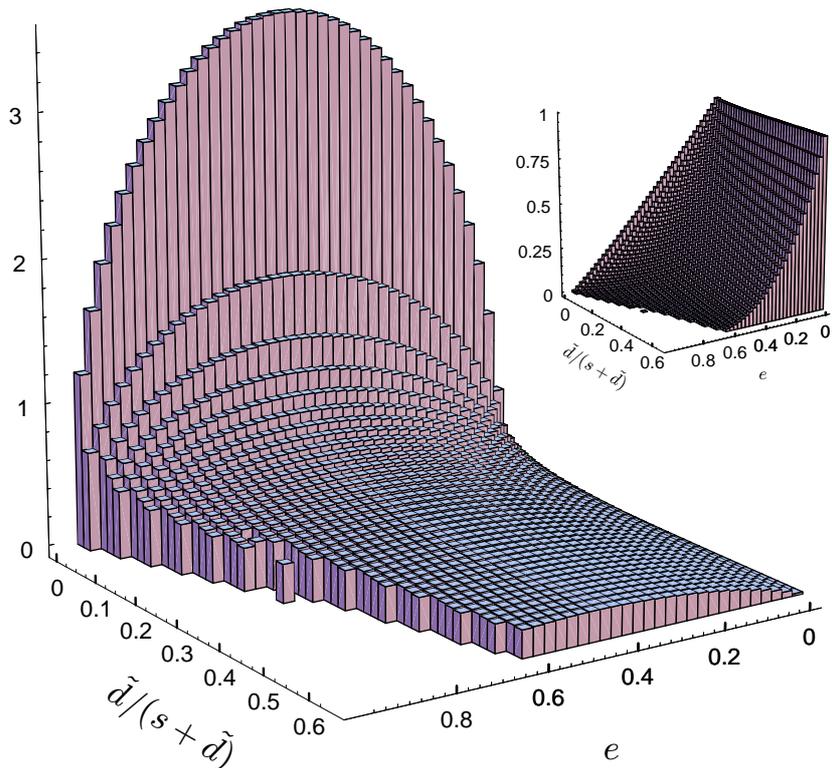


Figure 1: (a) CSS dispersal rates and (b) equilibrium population sizes at CSS in dependence on migration risk  $\tilde{d}/(s + \tilde{d})$  and extinction risk due to external disturbances  $e$  for logistic growth and large carrying capacities. Displayed dispersal rates are based on the deterministic model and therefore do not reflect the effects of demographic stochasticity. Notice that evolutionarily stable migration rates are maximal for intermediate extinction risks, whereas equilibrium population sizes decrease monotonically with extinction risk. By contrast, increased migration risks lead to monotonic decreases in evolutionarily stable migration rates as well as in equilibrium population sizes. In the absence of catastrophes, CSS dispersal rates are zero. Parameters:  $r = 1$ ,  $s = 0.5$ .

dispersal rates are not only evolutionarily stable strategies (ESS) but also continuously stable strategies (CSS) and that they can thus be regarded as the final outcomes of gradual evolutionary processes.

The results in Figure 1 demonstrate that the heuristic predictions sketched above were too simplistic. For low extinction risks, adapted dispersal rates indeed increase with higher rates of local extinction, thus confirming our expectations. For high rates of local extinction, however, adapted dispersal rates start to decrease again when extinctions become more frequent. In other words, evolutionarily stable rates of migration are maximal for intermediate extinction risks; around this maximum, adapted dispersal rates fall off when extinction risks are either increased or decreased. Such an intermediate maximum of dispersal rates has been observed in an analysis by Ronce *et al.* 2000. See also Karlson *et al.* (1995). The model in Ronce *et al.*, however, describes a metapopulation in discrete time, with natal dispersal and without a disperser pool. Moreover, the model by Ronce *et al.* does not allow for demographic stochasticity and is based on a restricted type of density regulation that simply imposes a ceiling on local population sizes. That the

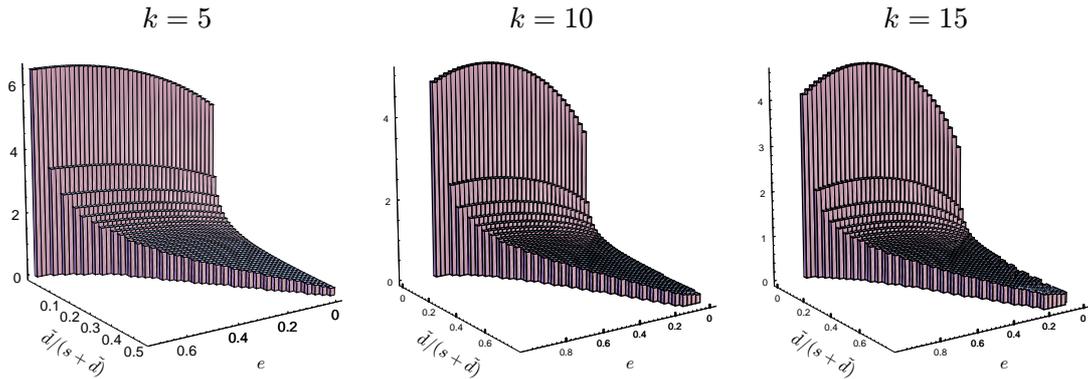


Figure 2: CSS dispersal rates for different levels of demographic stochasticity. Low carrying capacities  $k$  lead to large fluctuations in local population sizes and therefore select for positive CSS dispersal rates even in the absence of local extinction events. For the same reason, CSS dispersal rates are highest for low carrying capacities. For high carrying capacities, CSS dispersal rates converge towards the predictions of the deterministic model as shown in Figure 1. The white part of the bottom plane corresponds to inviable metapopulations. Parameters:  $r = 1$ ,  $s = 0.5$ ,  $d_0 = 0$ .

highlighted pattern of adaptation is found in two so different models of metapopulation dispersal underscores its potentially wide-ranging relevance.

## 4 Demographic stochasticity

We now address the question whether and to which extent the results presented in Figure 1 are affected by the simplifying assumption of ignoring the demographic stochasticity occurring within patches. This problem was actually flagged as unsolved in Ronce *et al.* 2000.

We therefore utilise the fully stochastic metapopulation dynamics introduced in Section 2, instead of relying on its deterministic approximation. The impact of demographic stochasticity on evolutionarily stable dispersal rates is expected to be strongest when local population sizes are small. For this reason, we explore adapted rates of migration for metapopulations with different local carrying capacities. The results presented in Figure 2 demonstrate that demographic stochasticity must not be ignored when predicting dispersal strategies. In particular for small rates of local extinction, systematic qualitative departures arise: under such conditions, selection favours much higher dispersal rates than expected. These discrepancies between deterministically-based and stochastically-based predictions are largest for small carrying capacities and occur for all combinations of migration risk and extinction risk. Not only does a decrease in local carrying capacities select for higher dispersal rates, it also reduces the domain of metapopulation viability, see Figure 2.

This surprising feature of metapopulation adaptation can be explained intuitively. If local populations exhibit deterministic growth, patches will fill up with individuals until their carrying capacity is exactly reached. There can be no overshooting of this capacity, neither can populations have smaller sizes unless a patch is reset by a local extinction event. In these circumstances, and if the frequency of empty patches is low, dispersal does not pay: the mortality cost of dispersal, combined with a low probability for finding a better patch, prevents evolutionarily stable dispersal rates to take off from zero. This is

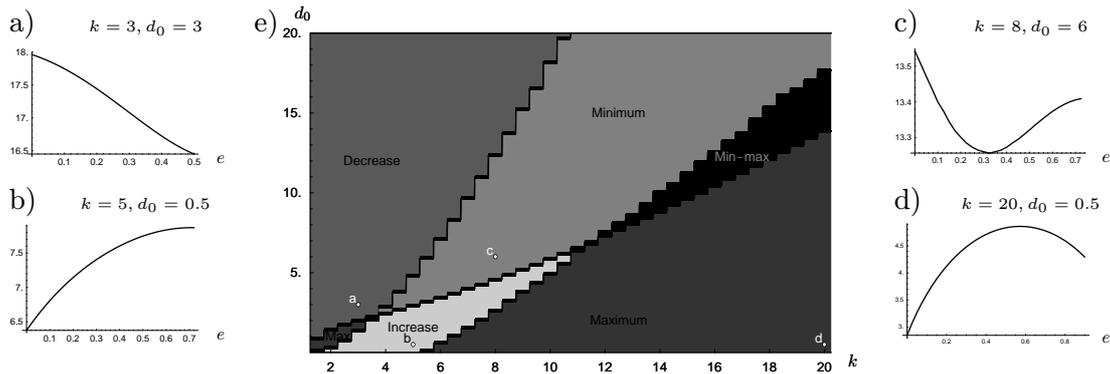


Figure 3: (a-d) Four different responses of CSS dispersal rates to variations in local extinction risks  $e$  due to external disturbances: (a) monotonic decrease, (b) monotonic increase, (c) intermediate minimum, and (d) intermediate maximum. In all four panels, variation of extinction risks extends over the range of viable metapopulations. (e) Parameter ranges that lead to the four types of behavior in dependence on carrying capacity  $k$  and demographic noise level  $d_0$ . The narrow ranges of more complicated cases, such as a local maximum followed by a local minimum, are marked with black lines. Parameter combinations corresponding to (a-d) are marked by black circles. Notice that the heuristically expected pattern of CSS dispersal rates increasing with extinction risks is confined to a very narrow band. Parameters:  $r = 1$ ,  $s = 0.5$ ,  $\tilde{d}/(s + \tilde{d}) = 0.005$ .

precisely what can be observed along the right-hand edge of Figure 1. However, as soon as local populations are subject to demographic stochasticity, the situation is different. Now local abundances will fluctuate around the carrying capacity of patches. Consequently, individuals in a non-empty patch always have a chance of finding better patches that are inhabited by fewer individuals. The fixed per capita cost of dispersal is thus counteracted by a benefit and, consequently, high rates of dispersal can evolve even for very low degrees of environmental disturbance.

Levels of demographic stochasticity are not only changed by variations in carrying capacities. Notice that growth rates of local populations are unaffected by modifying the sum of birth and death rates,  $b_n + d_n$ , as long as their difference,  $b_n - d_n$ , is preserved. In fact, the sum  $b_n + d_n$  measures the amount of demographic noise arising in local populations. We can therefore consider the same growth rates as, for example, in Figure 2 while increasing the level of demographic stochasticity by offsetting per capita birth and death rates by the same positive amount. Outcomes of metapopulation adaptation under such conditions are shown in Figure 3. For large ranges of parameters, we observe four kinds of behaviour with respect to increasing extinction risk: adapted dispersal rates can either increase or decrease monotonically with the risk of local extinction or they may exhibit an intermediate maximum or minimum. We also find a small range of parameter values where we have even more complicated case: a local maximum followed by a local minimum. See Figure 3 for details. The possibility for monotonically decreasing relations or for intermediate minima appears to have gone unnoticed in previous studies.

## 5 Alternative growth regimes

The results displayed in Figures 1, 2, and 3 are valid for metapopulations with locally logistic growth. Yet, we conjecture that the two patterns of metapopulation adaptation

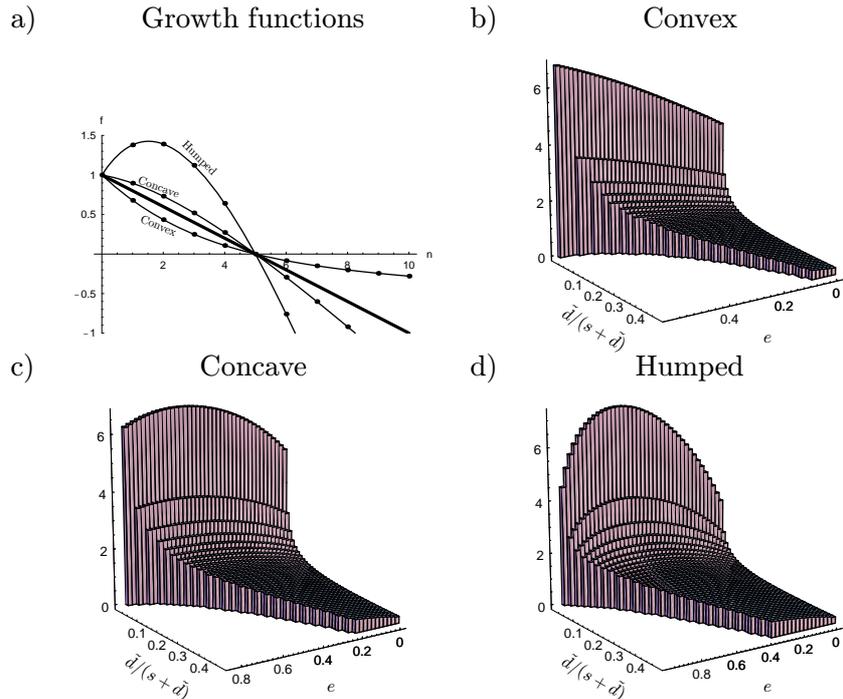


Figure 4: (a) Four different local growth regimes and corresponding growth functions  $f$ . The bold straight line characterizes logistic growth, as employed in Figure 2b. (b-d) CSS dispersal rates resulting from the three alternative different growth functions. Notice that in comparison with Figure 2b most qualitative features of dispersal evolution remain intact. However, intermediate maximization of CSS dispersal rates is less likely for convex growth functions. Parameters:  $k = 5$ ,  $s = 0.5$ ,  $d_0 = 0$ .

presented so far apply under a much wider range of ecological conditions.

To substantiate this claim, we analysed evolutionarily stable dispersal rates for different kinds of growth regimes. The characteristic feature of logistic density regulation is a linear dependence of per capita growth rates on population size. Instead of maintaining this somewhat artificial assumption (which, of course, is only supposed to serve as an approximation to the behaviour of real populations), we investigate three nonlinear dependencies, see Figure 4a. Results are presented in Figures 4b to 4d. We conclude that the considered departures from logistic growth kept intact both described patterns of metapopulation adaptation.

## 6 Discussion

In this paper we have evaluated the consequences of different metapopulation ecologies for the evolution of dispersal. We have aimed at incorporating into an individual-based model some features of metapopulation ecology as they are encountered in the field: demographic stochasticity and density regulation of local populations, migration of individuals at several stochastically determined moments during their lifetime, as well as randomly varying duration of migratory processes between patches, resulting in dispersal costs that vary across migration events. Under these conditions we have shown the existence of two patterns of metapopulation adaptation: dispersal rates do not necessarily increase with increased catastrophe rates, and relatively high dispersal rates can evolve for small local

populations with negligible extinction risks. We have demonstrated that both patterns are robust under a variety of local growth regimes.

The present study would have been impossible to conduct without the availability of recent results for determining the frequency-dependent fitness of strategies in metapopulation structures (see Appendices A and B). Instead of explicitly simulating the stochastic population dynamics of resident and potentially invading mutant phenotypes for a wide range of parameter values, all results in this paper are based on the direct computation of fitness values for mutant strategies in given resident environments. For this endeavour, the theory of adaptive dynamics (Metz *et al.* 1996; Dieckmann 1997; Geritz *et al.* 1997, 1998) has provided the appropriate framework, see also Appendix C.

Evidently, an attempt to incorporate 'realistic dynamics' into models of metapopulation evolution can amount to no more than a relative claim and therefore has to be interpreted against the backdrop of available literature. Although we propose that the present study allows for a much closer match between models of dispersal evolution and conditions actually encountered in the field, many simplifying assumptions remain to be overcome. To facilitate and encourage such extensions in the future, we provide a summary of issues that we suggest ought to be addressed.

1. First, connectivity structures and patch-size distributions of real metapopulations are certainly not uniform as has been assumed in our model. Patches tend to be connected by feasible migration routes to only a relatively small set of close-by patches; carrying capacities and demographic rates also tend to be heterogeneous across patches (Gyllenberg *et al.* 1997). In a similar vein, regional instead of global disperser pools could be considered to account for spatially bounded dispersal ranges.
2. An important second issue concerns the incorporation of sexual reproduction into models of metapopulation evolution. The repercussions of diploid inheritance, as opposed to the clonal reproduction assumed in the present paper, should be investigated. In this context, consideration of the dynamics of inbreeding depression is critical, as such depletion of local genetic variance can detrimentally affect the performance of small and relatively disconnected local populations. Another potential driving force of dispersal evolution is kin selection; here the study of genetic correlations emerging within and between patches is critical (see Gandon 1999 and Gandon & Michalakis 1999).
3. A further direction for future analysis is a systematic investigation of the effects of local growth regimes on metapopulation evolution. Although in this paper we could show the robustness of our findings for logistic growth and some variants, further exploration of alternative growth regimes is warranted. In particular, the consequences of Allee effects in local population dynamics should be addressed and are expected to result in modified or novel patterns of metapopulation adaptation.
4. In this paper we have assumed that rates of emigration, immigration, and local extinction are density-independent. Although this appears to be a reasonable assumption for many species and environments, a higher crash rate for large populations (resulting, for example, from the overexploitation of local resources) or density-dependent rates for leaving or entering patches (for animals with sufficiently developed perception skills) are entirely conceivable. For investigations in this direction see Gyllenberg & Metz (1999) and Metz & Gyllenberg (1999).
5. Finally, the metapopulation paradigm itself is based on the idealisation of a clear-cut dichotomy between habitable and nonhabitable patches of environment. In reality,

gradations of habitability are common and, moreover, the fine-structure of interactions within patches is likely to play a role.

The art of modelling in ecology is based on extracting from the complex reality of natural systems precisely those features that are most salient for understanding a given phenomenon or pattern. Unfortunately, this agenda urges us to comprehensively explore a wide variety of candidate features before we can decide which particular aspects deserve to be highlighted. The results advanced in this paper and the suggestions outlined above ought to be interpreted in this vein.

In addition to the list of steps for developing an increasingly adequate methodological foundation for the analysis of dispersal evolution, the importance of controlled empirical studies of metapopulation ecology and evolution can hardly be overestimated. We hope that the two patterns of metapopulation adaptation reported in this paper serve to stimulate such future developments.

## A Stochastic model and resulting invasion fitness

The general model and method for computing invasion fitness in metapopulations are described in Metz & Gyllenberg (1999). The model presented here differs from theirs by allowing for dispersal events throughout the lifetime of individuals, instead of considering natal dispersal.

In our model, a set of equivalent patches undergoes a Markov process with events for birth, death, dispersal, and local extinction. In the limit of infinitely many patches, the probability distribution  $p_n$  for a patch to have local population size  $n$  behaves deterministically:

$$\begin{aligned} \frac{d}{dt}p_0 &= -sDp_0 + (d_1 + m)p_1 + e(1 - p_0) , \\ \frac{d}{dt}p_n &= [sD + (n - 1)b_{n-1}]p_{n-1} - [n(b_n + m + d_n) + sD + e]p_n \\ &\quad + (n + 1)(d_{n+1} + m)p_{n+1} \text{ for } n > 0 , \\ \frac{d}{dt}D &= -sD + m \sum_{n=1}^{\infty} np_n - \tilde{d}D . \end{aligned} \quad (1)$$

The occupation  $D$  of the disperser pool is measured as the number of migrating individuals per patch. All other parameters are as explained in Section 2. In practice it is necessary to cut the summation in (1) at a value of  $n$  where  $np_n$  has become negligible because patches of that size are exceedingly rare.

The method for determining values of invasion fitness is based on first solving for the equilibrium  $\hat{p}_n$  of (1) for a given resident strategy.

The following equations then describe the dynamics of a small mutant population and are obtained from a linearization of (1). Occupation of the mutant disperser pool is measured by  $D'$ , while  $p'_{n,n'}$  denotes the fraction of patches that are inhabited by a combination of  $n$  resident and  $n'$  mutant individuals.

$$\begin{aligned} \frac{d}{dt}p'_{n,1} &= sD'\hat{p}_n + [sD + (n - 1)b_n]p'_{n-1,1} \\ &\quad - [(n + 1)d_{n+1} + nm + m' + sD + (n + 1)b_{n+1} + e]p'_{n,1} \\ &\quad + (n + 1)(d_{n+2} + m)p'_{n+1,1} + 2(d_{n+2} + m')p'_{n,2} , \end{aligned} \quad (2)$$

$$\begin{aligned} \frac{d}{dt}p'_{n,n'} &= [sD + (n - 1)b_{n+n'-1}]p'_{n-1,n'} + (n' - 1)b_{n+n'-1}p'_{n,n'-1} \\ &\quad - [(n + n')d_{n+n'} + nm + n'm' + sD + (n + n')b_{n+n'} + e]p'_{n,n'} \\ &\quad + (n + 1)(d_{n+n'+1} + m)p'_{n+1,n'} + (n' + 1)(d_{n+n'+1} + m')p'_{n,n'+1} , \end{aligned} \quad (3)$$

$$\frac{d}{dt}D' = - (s + \tilde{d})D' + m' \sum_{n=0}^{\infty} \sum_{n'=1}^{\infty} n'p'_{n,n'} . \quad (4)$$

Let  $\hat{p}'_{n,n'}$  be the equilibrium densities of  $p'_{n,n'}$  calculated from (2) and (3) for  $D' = 1$ . The Gauss-Seidel iteration method turned out to be most suitable for solving them. Then the quantity

$$R'_0 = \frac{m'}{s + \tilde{d}} \sum_{n=0}^{\infty} \sum_{n'=1}^{\infty} n' \hat{p}'_{n,n'} \quad (5)$$

is the metapopulation equivalent of the basic reproductive ratio of the mutant as it is familiar from ordinary population dynamics. Notice, however, that  $R'_0$  measures the increase in the mutant population size between dispersal events as opposed to between birth events. For given dispersal rates of resident and mutant,  $m$  and  $m'$ , the resulting invasion fitness is obtained as  $s_m(m') = \log R'_0$  and measures the expected long-term per capita growth rate of the small mutant population in the absence of density regulation.

## B Deterministic model and resulting invasion fitness

For large local populations, effects of demographic stochasticity can be neglected. We can then describe within-patch dynamics deterministically,

$$\frac{d}{dt}n = f(n)n - mn + sD = F(n, D). \quad (6)$$

The first term in the sum depends on the local growth regime, with per capita growth rates  $f(n)$ , while the second and third term describe the effects of emigration and immigration, respectively. In the case of logistic growth we choose  $f(n) = r(1 - n/k)$ .

Like in the stochastic model, the metapopulation state is described by the probability distribution  $p(n)$  of local population sizes, augmented by a measure for the occupation of the disperser pool:

$$\frac{\partial}{\partial t}p(n) + \frac{\partial}{\partial n}F(n, D)p(n) = -ep(n), \quad (7)$$

$$\frac{d}{dt}D = -(s + \tilde{d})D + m \int_0^\infty np(n)dn. \quad (8)$$

The boundary condition  $sDp(0) = e$  ensures that empty patches are filled at the same rate at which they are generated.

Gyllenberg & Metz (1999) derived an analytical expression for the invasion fitness of this metapopulation model. Here we reproduce one of their results in the notation of the present paper. Assume that we know the equilibrium occupation  $\hat{D}$  of the disperser pool. The maximal local population size is then  $\tilde{n}(\hat{D})$ , defined by  $F(\tilde{n}(\hat{D}), \hat{D}) = 0$ . For  $n$  between zero and  $\tilde{n}(\hat{D})$ , the equilibrium of (7) is given by

$$\hat{p}(n, \hat{D}) = e (F(n, \hat{D}))^{-1} \exp \left[ -e \int_0^n (F(\nu, \hat{D}))^{-1} d\nu \right]. \quad (9)$$

From  $\frac{d}{dt}\hat{D} = 0$  and (8),  $\hat{D}$  is determined by solving the equation

$$\hat{D} = \frac{m}{s + \tilde{d}} \int_0^{\tilde{n}(\hat{D})} n \hat{p}(n, \hat{D}) dn. \quad (10)$$

The expected per capita number of mutant dispersers produced by a local mutant population that was established when the cohabiting resident population had size  $n_0$  is

$$E'(n_0, D) = \int_{n_0}^{\tilde{n}(D)} \frac{m'}{F(n, D)} \exp \left( \int_{n_0}^n \frac{f(\nu) - m' - e}{F(\nu, D)} d\nu \right) dn. \quad (11)$$

From this, the metapopulation equivalent of the basic reproduction number of the mutant is obtained as

$$R'_0 = \frac{s}{s + \tilde{d}} \int_0^{\tilde{n}(\hat{D})} E'(n, \hat{D}) \hat{p}(n, \hat{D}) dn. \quad (12)$$

Like in Appendix A, the corresponding invasion fitness is given by  $s_m(m') = \log R'_0$ .

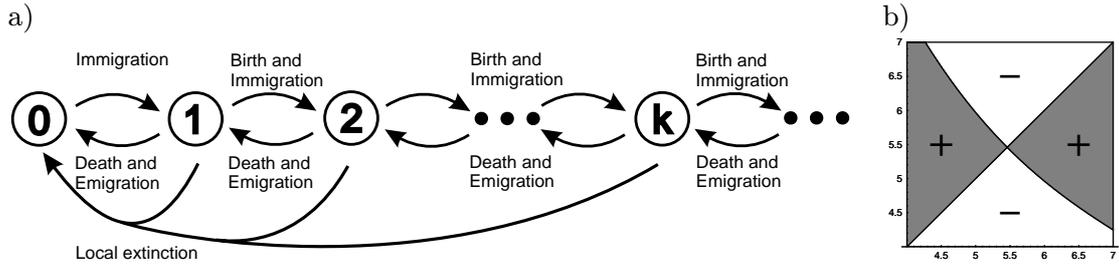


Figure 5: (a) Transition diagram for a single patch. Arrows describe the possible transitions in the state of the patch. Local population size is incremented by one by birth and immigration events and decreases by one when a death or emigration event occurs. Local extinction events can kill all individuals in a patch, thus resetting its population size to zero. At carrying capacity  $k$ , birth and death rates are equal. (b) Pairwise invasibility plot of dispersal rates. Gray regions correspond to combinations of resident and mutant dispersal rates,  $m$  and  $m'$ , that allow for mutant invasion. For these combinations, the invasion fitness  $s_m(m')$  is positive. In contrast, white regions correspond to negative signs and therefore to deleterious mutants. In the displayed plot, sequences of mutant invasion converge to a resident dispersal rate of  $m \approx 5.5$ . This strategy is also evolutionarily stable since  $s_m(m') < 0$  for all mutant strategies  $m'$ . The value  $m \approx 5.5$  therefore corresponds to a continuously stable strategy or CSS. Parameters:  $r = 1$ ,  $k = 7.5$ ,  $s = 0.5$ ,  $\tilde{d}/(s + \tilde{d}) = 0.005$ ,  $e = 0.8$ .

## C Procedure for determining CSS dispersal rates

In this paper we have used the framework of adaptive dynamics (Metz *et al.* 1996; Dieckmann 1997; Geritz *et al.* 1997, 1998) to predict outcomes of dispersal evolution. Based on the descriptions of invasion fitness derived in Appendices A and B, the evolutionary dynamics of the metapopulation can be analyzed by means of pairwise invasibility plots. In these plots, the sign of the invasion fitness  $s_m(m')$  is displayed in dependence on resident and mutant dispersal rates,  $m$  and  $m'$ , see the example in Figure 5b. Notice that results in this paper are all based on analytic fitness measures and not on the usual and slow method of indirectly estimating fitness values from the population dynamics of residents and mutants.

A strategy  $m^*$  is called convergence stable if the repeated invasion of nearby mutant strategies into nearby resident strategies will lead to the convergence of resident strategies towards  $m^*$ . This happens if, for a resident  $m$  and a mutant  $m'$  that are both close to  $m^*$ , we have  $s_m(m') > 0$  for  $m < m' < m^*$  and for  $m > m' > m^*$ . In contrast, a strategy  $m^*$  is called evolutionarily stable if it cannot be invaded by any other strategy  $m'$ , i.e. if  $s_{m^*}(m') < 0$  for all  $m'$ . Strategies that are both convergence stable and evolutionarily stable are called continuously stable strategies or CSSs (Eshel 1983). Such strategies are the expected final outcomes of the evolutionary process.

In Figure 5b, a CSS is located at  $m \approx 5.5$ . Notice that invasions will lead towards the CSS both from the left and from the right until, at the CSS, no further mutants can invade. All pairwise invasibility plots investigated in this study exhibited such CSSs. For identifying CSS dispersal rates we have utilized a bisection method to determine the zeros of  $\frac{\partial}{\partial m} s_m(m')|_{m'=m}$ , the selection gradient resulting from invasion fitness  $s_m(m')$ .

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