

Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity

K. PARVINEN,*† U. DIECKMANN,† M. GYLLENBERG*‡ & J. A. J. METZ†§

*Department of Mathematics, University of Turku, Turku, Finland

†Adaptive Dynamics Network, International Institute for Applied Systems Analysis, Laxenburg, Austria

‡Turku Centre for Computer Science, University of Turku, Turku, Finland

§Institute of Evolutionary and Ecological Sciences, Leiden, The Netherlands

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Abstract

In this paper, we predict the outcome of dispersal evolution in metapopulations based on the following assumptions: (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. 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. Second, we describe how demographic stochasticity affects the evolution of dispersal rates: evolutionarily stable dispersal rates remain high even when disturbance-related rates of local extinction are low, and a variety of qualitatively different responses of adapted dispersal rates to varied levels of disturbance become possible. This paper shows, for the first time, that evolution of dispersal rates may give rise to monotonically increasing or decreasing responses, as well as to intermediate maxima or minima.

Introduction

Metapopulations and their dynamics have become a central subject of conservation ecology and evolutionary ecology. By 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 (Nagy, 1996; Cadet, 1998; Gandon, 1999; Gandon & Michalakis, 1999; Parvinen, 1999, 2001; Ronce *et al.*, 2000a; Gyllenberg & Metz, 2001; Heino & Hanski, 2001; Metz & Gyllenberg, 2001; Kiski, 2002; Nagy, in press). 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 harmful 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. Yet, the ecological details assumed at both levels of population structure can qualitatively affect evolutionary outcomes. For this reason, it is important to investigate the evolution of 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.

In this paper, we investigate an evolutionary metapopulation model that incorporates more realistic

Correspondence: Kalle Parvinen, Department of Mathematics, University of Turku, Turku, FIN-20014, Finland.

Tel.: + 358 2 333 5623; fax: + 358 2 333 6595; e-mail: kalparvi@utu.fi

ecological detail into studies of dispersal evolution. We focus on three aspects.

First, most previous studies of dispersal evolution have relied either on Levins-type models (Levins, 1969, 1970), which ignore the within-patch dynamics of populations, or, instead, have assumed quite simple types of local population regulation, based on a ceiling for local population sizes (Olivieri *et al.*, 1995; Olivieri & Gouyon, 1997; Ronce *et al.*, 2000a; see also Hanski *et al.*, 1996; Hanski 1998). In the latter case, populations approach the ceiling without density regulation and then 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, 2001; Metz & Gyllenberg, 2001) our analysis is based 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 many 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 study metapopulation dynamics in continuous time, which is suitable when population growth is not seasonal. Obviously there

are also many ecological settings that are more adequately described by discrete-time models. For studies of metapopulations in discrete time, see Gyllenberg *et al.* (1993, 1996) and Hastings (1993).

The paper focuses on the question of how metapopulation dispersal responds to increased threats of local extinction. 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 dispersal, on the other hand, show a monotonically decreasing trend. Furthermore, it is demonstrated that the combination of demographic stochasticity and kin selection strongly affects evolutionarily stable dispersal strategies when local population sizes are small. The findings presented here show that deterministic models that ignore the implications of finite local populations can be qualitatively in error. We also 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.

Model description

We consider a metapopulation with a large number of 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. 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 . An individual thus has the probability $\tilde{d}/(s + \tilde{d})$ of dying during dispersal; we call this quantity the dispersal risk. Extinction of a local population due to external disturbances occurs at rate e . These events are illustrated in Fig. 1.

Within this ecological setting, we investigate the adaptation of the dispersal rate m . We assume that the number of patches is large enough for the entire metapopulation not to be liable to chance extinction by demographic stochasticity; otherwise, an evolutionarily stable dispersal rate obviously cannot be attained. Furthermore, the number of patches is assumed to be large enough for the metapopulation dynamics to be well approximated by one with infinitely many patches. Equations for this evolutionary metapopulation model are summarized 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

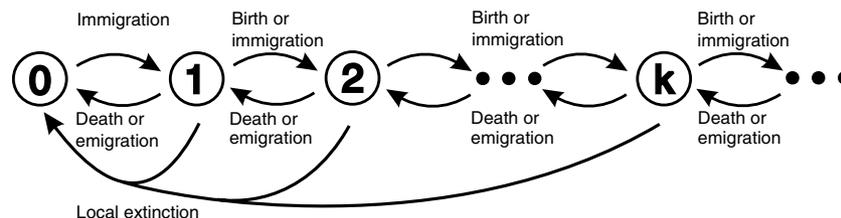


Fig. 1 Transition diagram for a single patch. Arrows describe the possible transitions in the state of the patch. Local population size is incremented by one by birth and immigration events and decreases by one when a death or emigration event occurs. Local extinction events can kill all individuals in a patch, thus resetting its population size to zero. At carrying capacity k , birth and death rates are equal.

a broad spectrum of variation, with some patches being overcrowded and others harbouring only small populations or being completely empty. Notice also that our model incorporates a simple kind of kin selection: individuals are likely to share patches with other individuals that are related by descent.

The growth of local populations is governed by density regulation. For simplicity, we assume that per capita birth rates are unaffected by density, $b_n = r$, and 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 also investigated.

Dispersal 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 of local populations. The former can be interpreted as a cost of dispersal and is thus expected to select for lower rates of dispersal. Local extinctions result in empty or thinly populated patches, which makes dispersal profitable. For this reason, increasing extinction risks are expected to select for higher dispersal rates. On the other hand, local extinctions make it impossible for a metapopulation to persist without dispersal, as already stated by Van Valen (1971).

We assess the validity of these predictions by systematically evaluating the evolutionarily stable dispersal rates under a range of dispersal 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; Parvinen, 1999; Gyllenberg & Metz, 2001; Metz & Gyllenberg, 2001) and facilitates the determination of evolutionarily stable strategies (ESSs). 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 the next section highlight the importance of demographic stochasticity and the danger of ignoring it in deterministic approximations.

Evolutionarily stable rates of dispersal, resulting from different risks of dispersal and extinction, are presented in Fig. 2. In Appendix C, we explain why the resulting dispersal rates are not only ESSs but also continuously stable strategies (CSSs) and that they can thus be regarded as the final outcomes of gradual evolutionary processes.

The results in Fig. 2 demonstrate that the 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 dispersal are maximal for intermediate extinction risks; around this maximum, adapted dispersal rates fall off when extinction risks are either increased or decreased. We suggest the following explanation for this. An increased rate of local extinction also affects the size structure of the metapopulation by decreasing the average population size and increasing the fraction of small local populations. Because the per capita growth rate $f(n)$ is a decreasing function of local population size n , patches with small local population size are the most advantageous. With the rate of local extinction increasing, more and more individuals thus reside in advantageous patches, which in turn decreases the benefit of dispersal.

An intermediate maximum of dispersal rates was also found by Ronce *et al.* (2000a), who suggested an explanation similar to ours for the observed pattern. Their model, however, describes a metapopulation in discrete time with instantaneous natal dispersal. Moreover, the model did not allow for demographic stochasticity and was based on a restricted type of density regulation imposing a ceiling on local population sizes.

As one may expect *a priori*, increased dispersal risk leads to a monotonic decline in evolutionarily stable dispersal rates. Notice, however, that this monotonicity

CSS dispersal rate

Population size at CSS

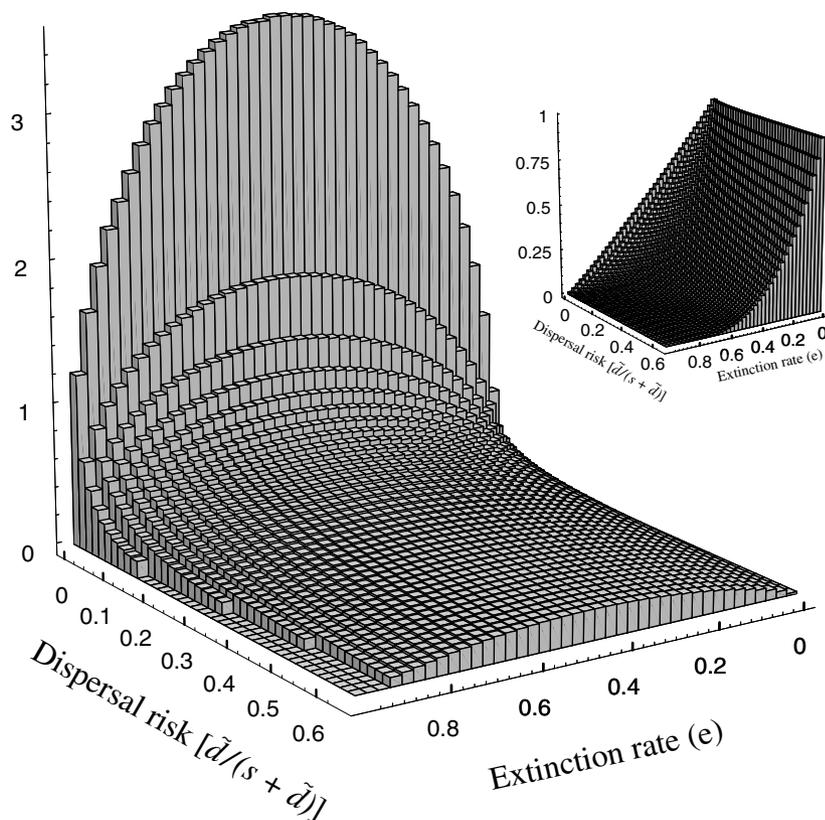


Fig. 2 (a) CSS dispersal rates and (b) equilibrium population sizes at CSS in dependence on dispersal risk $\tilde{d}/(s + \tilde{d})$ and extinction risk due to external disturbances e for logistic growth and large carrying capacities. Displayed dispersal rates are based on the deterministic model and therefore do not reflect the effects of demographic stochasticity. Notice that evolutionarily stable dispersal rates are maximal for intermediate extinction risks, whereas equilibrium population sizes decrease monotonically with extinction risk. By contrast, increased dispersal risks lead to monotonic decreases in evolutionarily stable dispersal rates as well as in equilibrium population sizes. In the absence of catastrophes, CSS dispersal rates are zero. Parameters: $r = 1$, $s = 0.5$.

has been demonstrated not to hold in some specific other models (Comins *et al.*, 1980; Gandon & Michalakis, 1999; Heino & Hanski, 2001). The mechanism responsible for this effect in Gandon & Michalakis (1999) is kin competition in newly founded populations when relatedness is high. The model in Heino & Hanski (2001) also involves kin competition, and once dispersal risk becomes so high that empty patches remain uncolonized for a long time, evolution favours increases migration rates. By contrast, in our model empty patches do not remain empty for a long time, since all patches can potentially be colonized from all other patches.

Demographic stochasticity

We now address the question whether and to which extent the results presented in Fig. 2 are affected by the simplifying assumption of ignoring the demographic stochasticity occurring within patches. This problem was flagged as unsolved in Ronce *et al.* (2000a), whereas an earlier study by Nagy (1996, in press) modelled the evolution of dispersal in Pica as a consequence of local demographic stochasticity only.

We, therefore, utilize the fully stochastic metapopulation dynamics introduced above, 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. When local population sizes are small, average relatedness among individuals is moderate or high and kin competition also plays a role. For this reason, we explore adapted rates of dispersal for metapopulations in dependence on the carrying capacity parameter k . The results (Fig. 3) demonstrate that demographic stochasticity must not be ignored when predicting dispersal strategies. In particular, for small rates of local extinction, selection favours much higher dispersal rates than expected. These discrepancies between deterministically based and stochastically based predictions are largest for small carrying capacity and occur for all combinations of dispersal 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 (Fig. 3). The change from a viable population with a positive CSS dispersal rate to a non-viable population happens through a bifurcation (Fig. 4).

This 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 reached. In these circumstances,

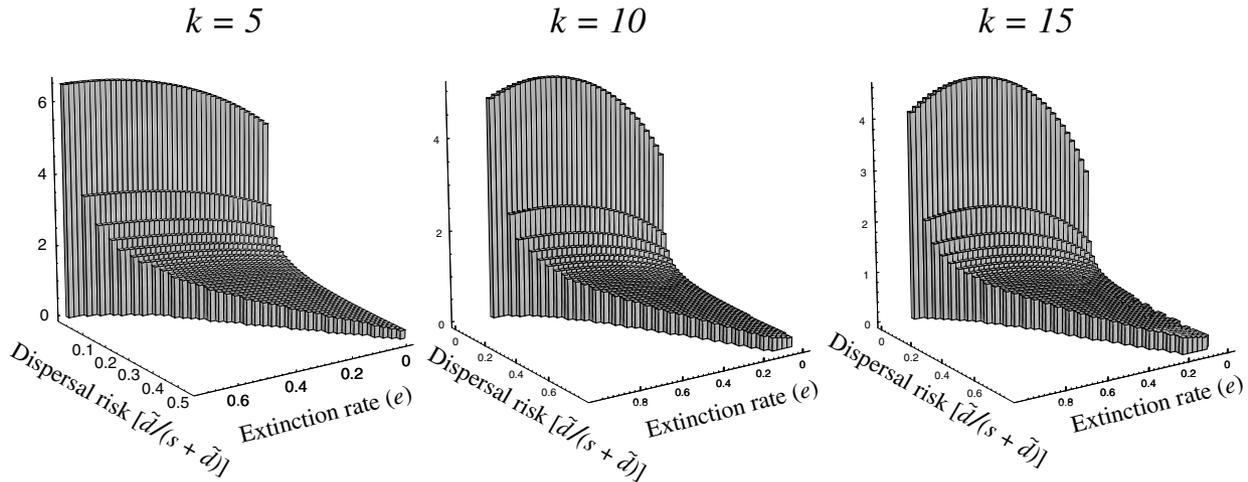


Fig. 3 CSS dispersal rates for different levels of demographic stochasticity. Low carrying capacities k lead to large fluctuations in local population sizes and therefore select for positive CSS dispersal rates even in the absence of local extinction events. For the same reason, CSS dispersal rates are highest for low carrying capacities. For high carrying capacities, CSS dispersal rates converge towards the predictions of the deterministic model as shown in Fig. 2. The white part of the bottom plane corresponds to unviable metapopulations. Parameters: $r = 1$, $s = 0.5$, $d_0 = 0$.

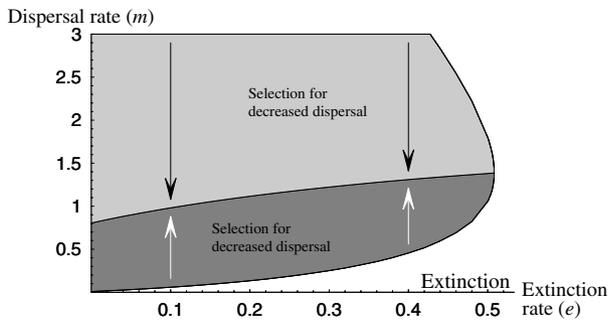


Fig. 4 Domain of population viability and the direction of selection in dependence on the catastrophe rate e . Beyond a bifurcation at $e \approx 0.5$ the metapopulation is no longer viable for any value of the dispersal rate m . The CSS dispersal rates are situated at the boundary between the light grey and dark grey areas. Parameters: $k = 5$, $r = 1$, $s = 0.5$, $d_0 = 0$, $\bar{d}/(s + \bar{d}) = 0.1$.

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 depart from zero. This is precisely what can be observed along the right-hand edge of Fig. 2. However, as soon as local populations are subject to demographic stochasticity, the situation is different. Now, local abundances will fluctuate around the carrying capacity. Consequently, individuals in a non-empty patch always have a chance of finding better patches that are inhabited by fewer individuals. In addition, individuals can escape kin competition by dispersing. 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 changes in the carrying capacity. 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 Fig. 3, although increasing the level of demographic stochasticity by offsetting per capita birth and death rates by the same positive amount d_0 . The per capita birth rate is then $b_n = r + d_0$ and the death rate is $d_n = rn/k + d_0$. The difference $f_n = b_n - d_n = r(1 - n/k)$ remains unchanged under variation of d_0 . Notice that values of k and d_0 can greatly differ between species and habitats. In particular, very small values of k are most likely to apply to metapopulations composed of territories, each of which can only sustain a few individuals.

Outcomes of metapopulation adaptation under such conditions show that for large ranges of parameters we observe four kinds of behaviour with respect to increasing extinction risk (Fig. 5): 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 an even more complicated case: a local maximum followed by a local minimum (Fig. 5). The possibility for monotonically decreasing relations or for intermediate minima appears to have gone unnoticed in previous studies. Some of

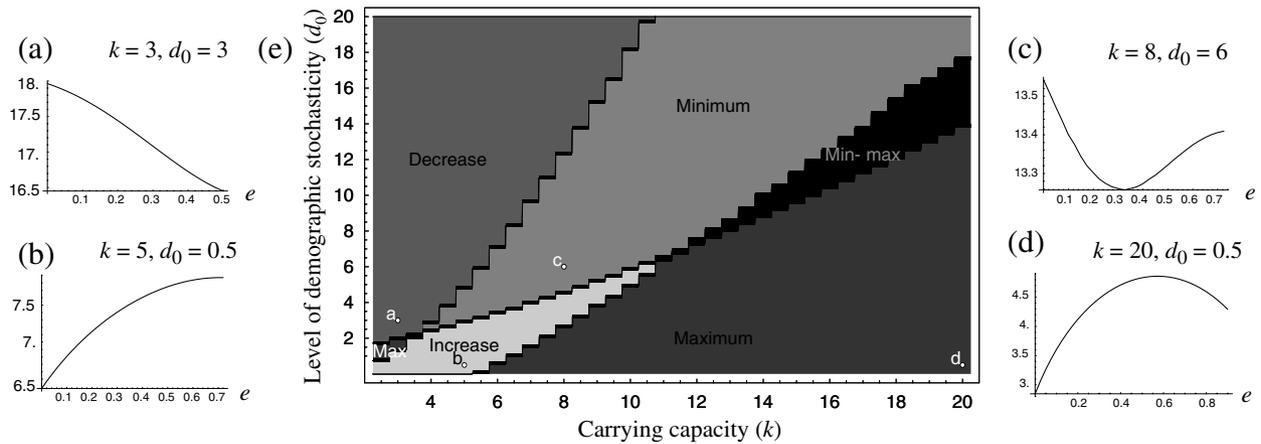


Fig. 5 (a–d) Four different responses of CSS dispersal rates to variations in local extinction risks e due to external disturbances: (a) monotonic decrease, (b) monotonic increase, (c) intermediate minimum and (d) intermediate maximum. In all four panels, variation of extinction risks extends over the range of viable metapopulations. (e) Parameter ranges that lead to the four types of behaviour 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: $r = 1$, $s = 0.5$, $\bar{d}/(s + \bar{d}) = 0.005$.

these responses occur only for relatively low values of k , although the case of an intermediate maximum dominates for large k and small d_0 .

Our interpretation is that the impact of demographic stochasticity and kin competition is smallest when the carrying capacity k is large and d_0 is small. This case is closest to the results without stochasticity, and we have an intermediate maximum in that case. Correspondingly, the impact of demographic stochasticity is largest when k is small and d_0 is large. In that case, when increasing the catastrophe rate, the effect of the decrease in average local competition for stayers outweighs the benefit for dispersers of reaching patches, which, on the average, are less crowded. Therefore, dispersal decreases with the rate of extinction risk e . Decreasing k and increasing d_0 does

not only increase demographic stochasticity, but also average relatedness and therefore kin competition (Fig. 6). Neither relatedness nor demographic stochasticity alone can explain the observed evolutionary patterns, because the contour lines in Fig. 6 cross the boundary curves in Fig. 5.

Alternative growth regimes

The results displayed in Figs 2, 3 and 5 are valid for metapopulations with local logistic growth. Yet, we expect the two patterns of metapopulation adaptation to apply to a much wider range of ecological conditions.

We analysed evolutionarily stable dispersal rates for different kinds of growth regimes. The characteristic

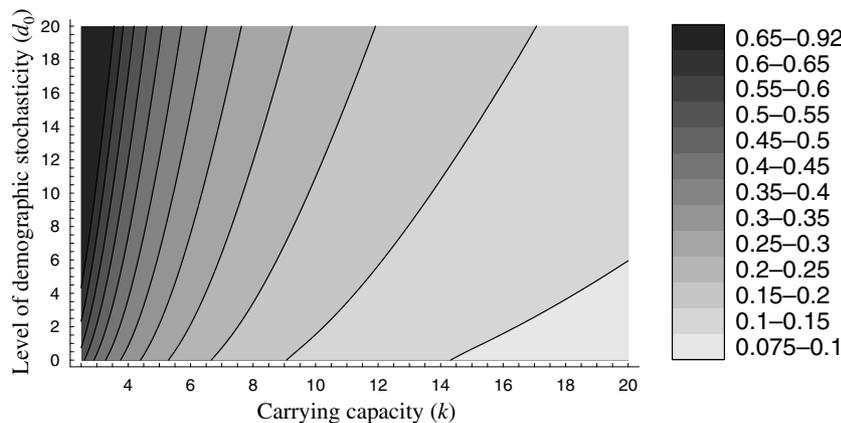


Fig. 6 Contour plot of relatedness at CSS with respect to the carrying capacity k and the level of demographic stochasticity d_0 . Dark colours correspond to higher values. Relatedness increases when k is decreased and when d_0 is increased. Parameters: $r = 1$, $s = 0.5$, $\bar{d}/(s + \bar{d}) = 0.005$.

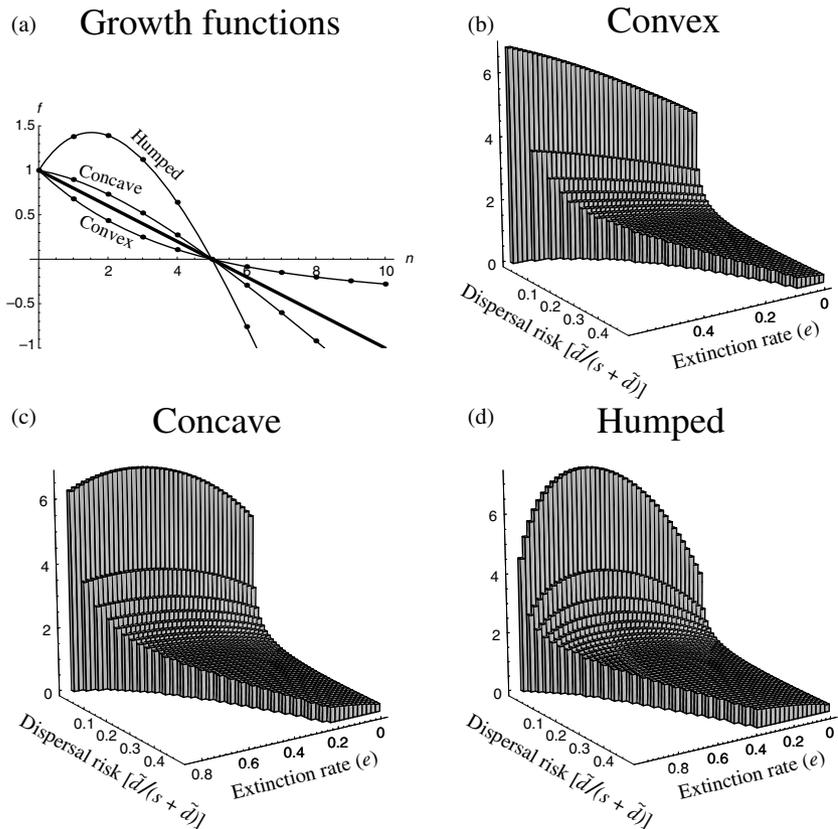


Fig. 7 (a) Four different local growth regimes and corresponding growth functions f . The bold straight line characterizes logistic growth, as employed in Fig. 3. (b–d) CSS dispersal rates resulting from the three alternative different growth functions. Notice that in comparison with Fig. 3 most qualitative features of dispersal evolution remain intact. However, intermediate maximization of CSS dispersal rates is less likely for convex growth functions. Parameters: $k = 5$, $s = 0.5$, $d_0 = 0$.

feature of logistic density regulation is a linear dependence of per capita growth rates on population size. We investigated three nonlinear dependencies (Fig. 7a). These departures from logistic growth did not alter the described patterns in metapopulation adaptation (Fig. 7b–d).

Discussion

Incorporation of demographic stochasticity and density regulation of local populations, dispersal of individuals at several stochastically determined moments during their lifetime, as well as randomly varying duration of migratory processes between patches, result in dispersal costs that vary across dispersal events. Under these conditions, two patterns of metapopulation adaptation exist: 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. Both patterns are robust under a variety of local growth regimes.

The present study uses recent results for determining the frequency-dependent fitness of strategies in structured metapopulations (Appendices A and B). Instead of simulating the stochastic population dynamics of resident

and potentially invading mutant phenotypes for a wide range of parameter values, fitness values for mutant strategies in given resident environments are computed. The theory of adaptive dynamics (Metz *et al.*, 1996; Dieckmann, 1997; Geritz *et al.*, 1997, 1998) has provided the appropriate framework for finding the ESSs (Appendix C).

Although the present models provide a closer match to conditions actually encountered in the field, many simplifying assumptions remain present. A number of issues ought to be addressed in future models.

1. Patches tend to be connected by feasible dispersal 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; Parvinen, 2002). In a similar vein, regional instead of global disperser pools could be considered to account for spatially bounded dispersal ranges.
2. ESSs realized by a population that is homozygous on the relevant loci coincide with those calculated for a clonal model like ours, as the invasion propensity of any mutant allele is fully determined by its heterozygotes. However, if patch sizes are small, mutant homozygotes appear, even though the proportion of

mutants in the population as a whole is still infinitesimally small. Implications of this finite-size effect depend on genetic detail and thus calls for closer investigation. In finite and sufficiently small populations, we may also have to account for the consequences of inbreeding depression resulting from the local depletion of genetic variance. For a discussion of (kin) selection in Mendelian metapopulations, see Gandon (1999) and Gandon & Michalakis (1999).

3. Further exploration of alternative growth regimes is warranted. In particular, the consequences of Allee effects in local population dynamics can be addressed and have been shown to result in novel patterns of metapopulation adaptation (Gyllenberg *et al.*, 2002).
4. In this paper, it was assumed that rates of emigration, immigration, and local extinction are density-independent. Although a reasonable assumption for many species and environments, a higher crash rate for large populations (resulting, e.g. from the overexploitation of local resources) or density-dependent rates for leaving or entering patches (for animals with sufficiently developed perception skills) are also conceivable. For investigations in this direction, see Gyllenberg & Metz (2001), Metz & Gyllenberg (2001) and Gyllenberg *et al.* (2002).
5. Most earlier studies have investigated dispersal evolution independently of other life-history traits (for exceptions see Kisdi 2002; Ronce *et al.*, 2000b). It would be of particular interest to consider the joint evolution of dispersal rates and morphological or physiological traits that lower the risk of dispersal at the cost of reduced local competitive ability or growth rate.
6. Finally, the metapopulation paradigm itself is based on the idealization 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.

In addition to these steps for advancing the theoretical foundation of the evolution of dispersal, the importance of controlled empirical studies of metapopulation ecology and evolution can hardly be overemphasized. We hope that the two patterns of metapopulation adaptation reported in this paper serve to stimulate such future developments.

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Appendix A: Stochastic model and resulting invasion fitness

The general model and method for computing invasion fitness in metapopulations are described in Metz & Gyllenberg (2001). 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, populations inhabit equivalent patches in which the local population undergoes a Markov process with events for birth, death, dispersal and local extinction. See Fig. 1 for illustration. In the limit of infinitely many patches, the probability distribution p_n for a patch to have local population size n behaves deterministically:

$$\begin{aligned} \frac{d}{dt}p_0 &= -sDp_0 + (d_1 + m)p_1 + e(1 - p_0), \\ \frac{d}{dt}p_n &= [sD + (n - 1)b_{n-1}]p_{n-1} - [n(b_n + m + d_n) + sD + e]p_n \\ &\quad + (n + 1)(d_{n+1} + m)p_{n+1} \text{ for } n > 0, \\ \frac{d}{dt}D &= -sD + m \sum_{n=1}^{\infty} np_n - \tilde{d}D. \end{aligned} \tag{A1}$$

The occupation D of the disperser pool is measured as the number of migrating individuals per patch. All other parameters are as explained in the main text. We assume that births and deaths happen one at a time, with the exception of a local catastrophe killing all individuals in a patch. In practice, it is necessary to cut the summation in (1) at a value of n where np_n has become negligible because local populations of that size are exceedingly rare. We have used the value $K = 2k$.

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. A mutant disperser has the probability $\hat{p}_n s / (s + \tilde{d})$ to end up in an $(n, 0)$ -patch, turning it into an $(n, 1)$ -patch. The newly founded colony undergoes a Markovian stochastic population process until extinction. Extinction of such a colony can result from a catastrophe killing the whole local population, or from demographic stochasticity bringing the number of mutants to zero. The rate at which a patch with size (n, n') becomes a patch with size $(n, n' + 1)$ is $c_{n,n'}^{0,+}$ etc. The subscript (n, n') refers to a patch that initially has n resident and n' mutant individuals, whereas the superscript $(0, +)$ indicates that the number of resident individuals resulting from the considered type of event remains unchanged whereas the number of mutant individuals is increased by 1. The values are

$$\begin{aligned} c_{n,n'}^{0,+} &= n' b_{n+n'}, \\ c_{n,n'}^{0,-} &= n' (d_{n+n'} + m'), \\ c_{n,n'}^{+,0} &= sD + n b_{n+n'}, \\ c_{n,n'}^{-,0} &= n (d_{n+n'} + m), \end{aligned}$$

$$c_{n,n'}^{0,0} = (n + n') d_{n+n'} + n m + n' m' + sD + (n + n') b_{n+n'} + e \quad (\text{A2})$$

for $n \geq 0$ and $n' \geq 1$, because a mutant colony has at least one mutant.

Now, we determine the mean total time $u_{n,n'}$ that a local mutant colony spends in state (n, n') before going extinct. Let $v_{n,n'} = c_{n,n'}^{0,0} u_{n,n'}$. The numbers $v_{n,n'}$ can be interpreted as the number of times the colony passes through state (n, n') . They can be calculated using the Jacobi iteration method, that is, as the limit $v_{n,n'}(\infty)$ from the recurrence

$$\begin{aligned} v_{n,n'}(t+1) &= \frac{c_{n,n'+1}^{0,-}}{c_{n,n'+1}^{0,0}} v_{n,n'+1}(t) + \frac{c_{n-1,n'}^{+,0}}{c_{n-1,n'}^{0,0}} v_{n-1,n'}(t) \\ &+ \frac{c_{n+1,n'}^{-,0}}{c_{n+1,n'}^{0,0}} v_{n+1,n'}(t) + \frac{c_{n,n'-1}^{0,+}}{c_{n,n'-1}^{0,0}} v_{n,n'-1}(t) \end{aligned} \quad (\text{A3})$$

for $n \geq 0, n' \geq 1, n + n' \leq K$ with the boundary conditions $v_{n,0} = \hat{p}_n s / (s + \hat{d})$, $v_{-1,n'} = 0$ and $v_{i,K+1-i} = 0$ together with the convention $c_{n,0}^{0,+} = 1$ and $c_{n,0}^{0,0} = 1$. We used the Gauss-Seidel version of recurrence (3) to make the computation faster.

Having determined the times $v_{n,n'}$, the quantity

$$R'_0 = m' \sum_{n=0}^{K-1} \sum_{n'=1}^{K-n} n' \hat{u}'_{n,n'} = m' \sum_{n=0}^{K-1} \sum_{n'=1}^{K-n} \frac{n' \hat{v}'_{n,n'}}{c_{n,n'}} \quad (\text{A4})$$

is the metapopulation-equivalent of the basic reproduction 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 $s_m(m')$ is sign-equivalent with $\log R'_0$ and measures the expected long-term per capita growth rate of the small mutant population in the absence of density regulation.

The procedure described above can also be used for the calculation of average relatedness. As the quantity $\hat{u}'_{n,n'}$ is the mean total time a colony spends in state (n, n') at the population dynamical equilibrium, the average relatedness r is

$$r = \frac{\sum_{n=0}^{K-1} \sum_{n'=1}^{K-n} n' (n' / (n + n')) \hat{u}'_{n,n'}}{\sum_{n=0}^{K-1} \sum_{n'=1}^{K-n} n' \hat{u}'_{n,n'}} \quad (\text{A5})$$

This average relatedness gives an indication of the extent to which kin selection potentially affects the evolution of dispersal rates. However, it is not possible to use it in an inclusive fitness argument, as individuals experiencing different circumstances (patch compositions) do not vary independently in their expected fitness payoff and relatedness. Fortunately, there is no need for such an

argument, as the overall fitness measure R_0 captures all direct and indirect fitness contributions of an individual's strategy in one go.

Appendix 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,

$$\frac{d}{dt} n = f(n)n - mn + sD = F(n, D). \quad (\text{B1})$$

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

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

$$\frac{\partial}{\partial t} p(t, n) + \frac{\partial}{\partial n} [F(n, D)p(t, n)] = -ep(t, n), \quad (\text{B2a})$$

$$\frac{d}{dt} D = -(s + \hat{d})D + m \int_0^\infty np(t, n) dn. \quad (\text{B2b})$$

The side condition

$$sDp(t, 0) = e \int_0^\infty p(t, n) dn \quad (\text{B2c})$$

of the partial differential equation (B2a) ensures that empty patches are filled at the same rate at which they are generated. From (B2a) and (B2c) we get $\frac{d}{dt} \int_0^\infty p(t, n) dn = 0$ and thus $\int_0^\infty p(t, n) dn = 1$.

Gyllenberg & Metz (2001) 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 $\hat{n}(\hat{D})$, defined by $F(\hat{n}(\hat{D}), \hat{D}) = 0$. For n between zero and $\hat{n}(\hat{D})$, the equilibrium of (B2a) is given by

$$\hat{p}(n, \hat{D}) = e(F(n, \hat{D}))^{-1} \exp \left[-e \int_0^n (F(v, \hat{D}))^{-1} dv \right]. \quad (\text{B3})$$

From $\frac{d}{dt} \hat{D} = 0$ and (B2b), \hat{D} is determined by solving the equation

$$\hat{D} = \frac{m}{s + \hat{d}} \int_0^{\hat{n}(\hat{D})} n \hat{p}(n, \hat{D}) dn. \quad (\text{B4})$$

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

$$E'(n_0, D) = \int_{n_0}^{\tilde{n}(D)} \frac{m'}{F(n, D)} \exp\left(\int_{n_0}^n \frac{f(v) - m' - e}{F(v, D)} dv\right) dn. \tag{B5}$$

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

$$R'_0 = \frac{s}{s + \bar{d}} \int_0^{\tilde{n}(\hat{D})} E'(n, \hat{D}) \hat{p}(n, \hat{D}) dn. \tag{B6}$$

A simple and effective procedure for the numerical calculation of the required integrals can be found in Metz & Gyllenberg (2001); see also Parvinen (2002).

Appendix 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 the appendices above, the evolutionary dynamics of the metapopulation can be analysed by means of pairwise invasibility plots (Van Tienderen & De Jong, 1988). 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 Fig. A1. Notice that results in this paper are all based on analytic fitness measures and not on the often 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

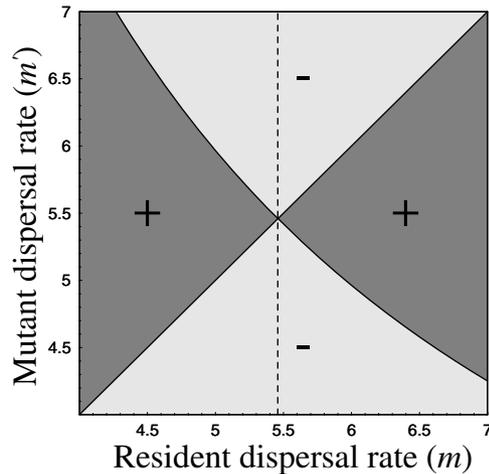


Fig. A1 Grey regions correspond to combinations of resident and mutant dispersal rates, m and m' , that allow for mutant invasion. For these combinations, the invasion fitness $s_m(m')$ is positive. In contrast, white regions correspond to negative signs and therefore to deleterious mutants. In the displayed 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 CSS. Parameters: $r = 1$, $k = 7.5$, $s = 0.5$, $\bar{d}/(s + \bar{d}) = 0.005$, $e = 0.8$.

cannot be invaded by any other strategy m' , i.e. if $s_{m^*}(m') < 0$ for all $m' \neq m^*$. 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 Fig. A1, 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 $s_m(m')$.