

# Local Extinction and the Evolution of Dispersal Rates: Causes and Correlations

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**ABSTRACT:** We present the results of individual-based simulation experiments on the evolution of dispersal rates of organisms living in metapopulations. We find conflicting results regarding the relationship between local extinction rate and evolutionarily stable (ES) dispersal rate depending on which principal mechanism causes extinction: if extinction is caused by environmental catastrophes eradicating local populations, we observe a positive correlation between extinction and ES dispersal rate; if extinction is a consequence of stochastic local dynamics and environmental fluctuations, the correlation becomes ambiguous; and in cases where extinction is caused by dispersal mortality, a negative correlation between local extinction rate and ES dispersal rate emerges. We conclude that extinction rate, which both affects and is affected by dispersal rates, is not an ideal predictor for optimal dispersal rates.

**Keywords:** dispersal rate, extinction rate, population extinction, metapopulation, evolutionary modeling, individual-based model.

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Studies on the evolution of animal dispersal have mostly been based on rather general considerations of the trade-off between the costs and benefits of dispersal (Levin et al. 1984; Johnson and Gaines 1990; McPeck and Holt 1992). Avoidance of kin competition is probably the most general reason to promote dispersal (Hamilton and May 1977; Comins et al. 1980; Gandon and Michalakis 1999; Ronce et al. 2000*b*). However, environmental fluctuations and habitat dynamics (Venable and Brown 1993; Travis and Dytham 1998), local population extinction (van Valen 1971; Olivieri et al. 1995; Ronce et al. 2000*a*), late suc-

cessional status (Ronce and Olivieri 1997), differences in patch capacity (McPeck and Holt 1992; Poethke and Hovestadt 2002), differences in population density (Ruxton 1996; Jánosi and Scheuring 1997; Sæther et al. 1999; Travis et al. 1999; Metz and Gyllenberg 2001; Poethke and Hovestadt 2002), and the occurrence of autocorrelated habitat distribution (Hovestadt et al. 2001) are also factors promoting the evolution of dispersal.

Among the potential benefits for a dispersing individual, the chance to arrive in a hitherto unoccupied patch and thus become a founder of a new population is the most appealing of all. Since the number of empty patches should increase with increasing extinction rate, a number of studies have been devoted to the relationship between local extinction rates and individual dispersal rates (for a review, see Ronce et al. 2000*a*). Most of them show that we should expect evolutionarily stable (ES) dispersal rates to increase with local extinction rates (e.g., Comins et al. 1980; Olivieri et al. 1995). This prediction has been neatly confirmed by numerous comparative studies on the influence of habitat stability on the propensity of individuals to disperse (e.g., Southwood 1962; Denno et al. 1991; Roff 1994). While species living in ephemeral habitats show high dispersal rates, species in stable habitats tend to remain in their natal sites.

Recently, Ronce et al. (2000*a*) and Parvinen et al. (2003) have challenged this simple view of the relationship between local extinction rate and ES dispersal rate. They suggest that, under some conditions, ES dispersal rates may in fact decrease as local extinction rates decrease. At low rates of population growth, frequent extinction will bring about small mean population sizes as most occupied patches recover from a recent extinction event. In such a situation, local competition is usually low, and consequently, selection for emigration is reduced.

There is another shortcoming in the assumption of a simple relationship between extinction rates and ES dispersal rates. It ignores the fact that extinction is in part an emergent property of the dispersal process itself (Lande 1988; Hanski and Zhang 1993); that is, dispersal behavior may influence local and global extinction risk of a species

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(Thomas 2000; Hanski 2001). On the one hand, extinction risk of (small) local populations may be increased by the loss of individuals through emigration (Fagan et al. 1999); on the other hand, extinction risk may be reduced by the influx of immigrants (the “rescue effect”; Brown and Kodric-Brown 1977; Hanski 1999). We thus suspect that the relationship between extinction rate and dispersal rate critically depends on factors like landscape configuration, dispersal mortality, frequency of environmental catastrophes, population dynamics, and density dependence of dispersal.

In this article, we want to investigate the relationship between population extinction and dispersal rate with extinction driven by different mechanisms. Our analysis builds on an individual-based model simulating the evolution of dispersal strategies in metapopulations, as presented in Poethke and Hovestadt (2002). In a number of simulation experiments, we will manipulate local extinction rates by alteration of the frequency of environmental catastrophes, the intensity of environmentally induced fluctuations in fertility, and dispersal mortality. Based on these experiments, we will show that there is no general relationship between local extinction rate and ES dispersal rate and that extinction rate thus is not an ideal predictor of dispersal.

### The Model

Our simulation experiments are based on an individual-based model of insect dispersal in patchy landscapes of  $n_{\text{patch}}$  habitat patches with variable capacities  $K_i$ . Mean patch capacity was  $K = 100$  individuals. To allow for a broad range of local extinction rates, values of  $K_i$  were taken from a uniform distribution with  $10 \leq K_i \leq 190$ .

Each individual is characterized by its sex, its affiliation with a specific patch ( $i$ ), and by four alleles at two different diploid loci that determine density dependence ( $p_C$ ) and patch-size dependence ( $p_K$ ) of the individual’s dispersal probability  $d$ . In our model, individuals simultaneously disperse before mating and production of offspring; each individual has only one opportunity to disperse. Dispersing individuals die with a probability  $\mu$ , regardless of patch origin.

Local population dynamics are governed by density-dependent reproduction of individuals. After mating with a local male, a female gives birth to  $\Lambda$  offspring, where  $\Lambda$  is a Poisson-distributed number with a patch- and time-specific mean,  $\Lambda_{\text{mean}}(t, \text{patch})$ . For each generation, the value of  $\Lambda_{\text{mean}}(t, \text{patch})$  is drawn from a lognormal distribution with mean  $\lambda$  and a standard deviation  $\sigma$ , the latter determining the degree of environmental fluctuations. Environmental fluctuations are assumed to be uncorrelated in space and time. Offspring develop into mature individuals with a density-dependent survival probability  $s$ :

$$s = \frac{1}{1 + aN_i}, \quad (1)$$

with  $a = (\lambda - 1)/K$ ,  $N_i$  = population size in patch  $i$ , and  $K_i$  = carrying capacity of patch  $i$ .

After all individuals have reached maturity, they disperse in proportion to their individual dispersal probability  $d$ . We assume global dispersal; that is, a successful disperser reaches any patch in the landscape (except its home patch) with the same probability ( $1/[n_{\text{patch}} - 1]$ ). In our simulations, dispersal probability is sensitive to local patch size and density according to the nonlinear model of Poethke and Hovestadt (2002):

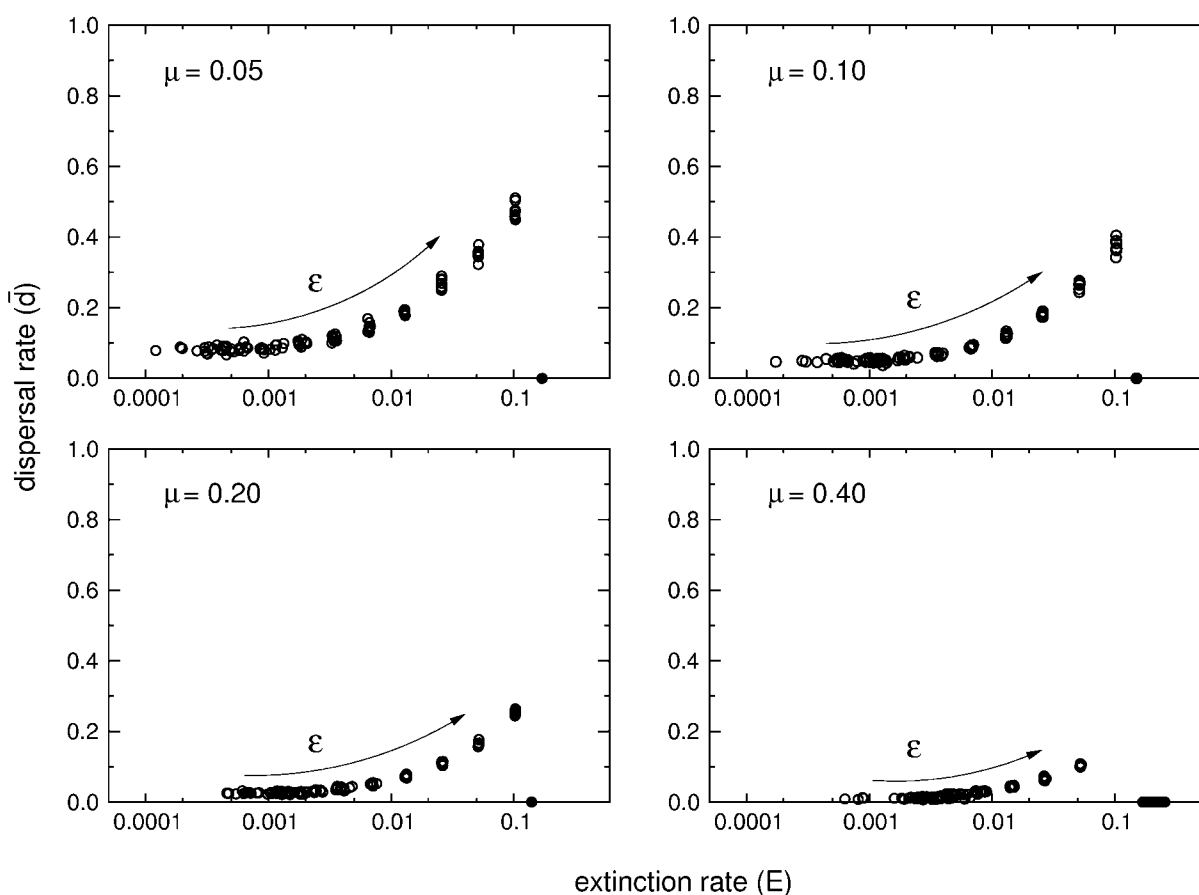
$$d = \begin{cases} 0 & \text{if } C_i \leq C_{\text{th}} \\ 1 - \frac{1}{C_i} \left( p_C - \frac{p_K}{k_i} \right) & \text{if } C_i > C_{\text{th}} \end{cases} \quad (2)$$

with  $C_i$  = population density in patch  $i$ ,  $k_i = K_i/K_{\text{mean}}$  relative capacity of patch  $i$ ,  $K_{\text{mean}}$  = mean carrying capacity of patches in the landscape, and  $C_{\text{th}} = p_C - (p_K/k_i)$  patch-size-dependent threshold density.

The individual values for  $p_C$  and  $p_K$  are determined by the mean value of the two corresponding alleles. At initiation, values for the alleles coding for  $p_C$  and  $p_K$  are set to 1 and 0, respectively. The values for these alleles may change by mutation, thus allowing for the evolution of density- and patch-size-dependent dispersal strategies. To promote greater variability of genotypes in the first generations and to reduce the influence of mutations on the stability of the final result, we let mutation rates exponentially decrease from  $\sim 0.1$  to  $< 0.001$  over the course of the simulation experiments (10,000 generations; for details, see Poethke and Hovestadt 2002). For a broad range of parameters, we compared the results of this procedure with results generated by simulations with small constant mutation rates. In all cases, both approaches produced completely similar results.

The frequency of local extinction ( $E$ ) is a result of either external catastrophes, which occur at a given frequency ( $\epsilon$ ) and lead to the extinction of a patch regardless of the actual population size, or of random fluctuations in population size. The latter are the combined result of environmentally caused fluctuations in offspring number ( $\sigma$ ) and demographic stochasticity. To analyze differences in the influence of these mechanisms on the evolution of dispersal rates, simulation experiments were run under two different scenarios.

*Environmental catastrophes.* In this scenario, we assume that all populations face the same externally determined extinction risk, independent of patch capacity or actual population size. This is realized by randomly destroying



**Figure 1:** Mean evolutionarily stable dispersal rate ( $\bar{d}$ ) after 10,000 generations as a function of local extinction rate ( $E$ ) in the environmental catastrophe scenario, with extinction driven by external catastrophes ( $0 \leq \epsilon < 0.11$ ). Simulation runs are categorized according to dispersal mortality ( $\mu$ ). For each set of parameter combinations, the results of nine replicate simulation runs are shown. Dots on baseline indicate metapopulations that did not persist for 10,000 generations.

populations with a given probability  $\epsilon$  ( $0 < \epsilon \leq 0.1$ ). To minimize the rate of extinction by demographic fluctuations, environmental conditions were assumed to be constant ( $\sigma = 0$ ) in this scenario.

*Fluctuating environment.* In this scenario, local extinction is caused by demographic stochasticity and environmentally caused fluctuations ( $0 < \sigma \leq 9.75$ ) of offspring number ( $\Lambda$ ) while  $\epsilon$  is set to 0.

In both scenarios, we run simulations with different values for dispersal mortality ( $\mu$ ) to account for both the direct effects of dispersal risk on dispersal rates and its indirect effect on extinction.

## Results

In the simulations, population mean dispersal rates usually approached equilibrium after less than 2,000 generations, even though it sometimes took 6,000 generations before

the two behavioral parameters,  $p_C$  and  $p_K$ , settled at approximately stable values. The results of our simulation experiments show that dispersal mortality ( $\mu$ ), the strength of environmental fluctuations ( $\sigma$ ), and the frequency of environmental catastrophes ( $\epsilon$ ) all have a strong influence on evolutionarily stable (ES) dispersal rates. Depending on the values of these parameters, ES dispersal rates after 10,000 generations scattered widely between values close to 0 and values beyond 0.6.

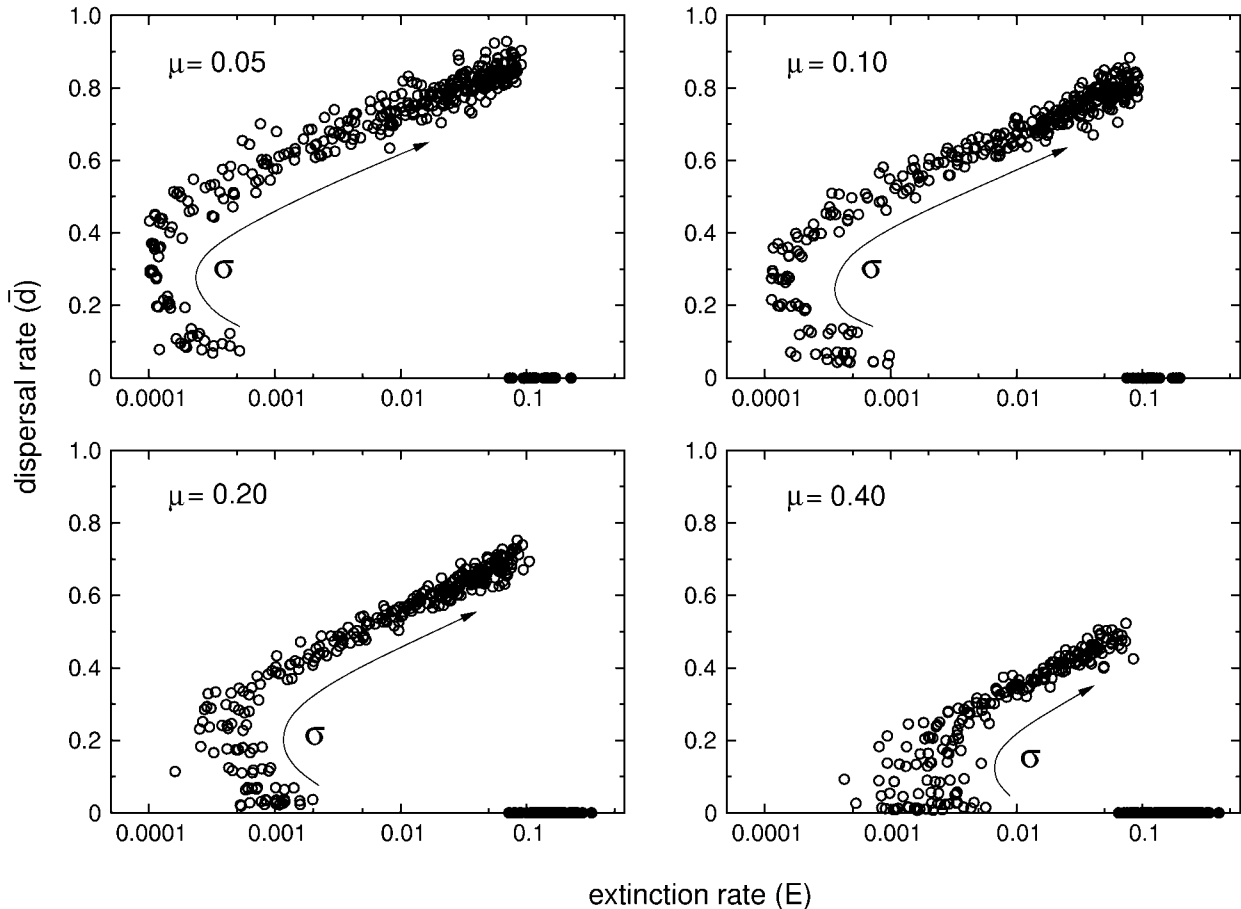
For the environmental catastrophe scenario ( $\epsilon > 0$ ;  $\sigma = 0$ ), local extinction can principally result either from external disturbances (with frequency  $\epsilon$ ) or from demographic fluctuations in population size. Given the large value of  $K_{\text{mean}}$  ( $= 100$ ), demographic fluctuations are in fact of minor importance in our simulations in this scenario; that is,  $E \approx \epsilon$ . The ES dispersal rates increase with increasing frequency of local extinction ( $E$ ) and decrease with increasing dispersal mortality ( $\mu$ ; fig. 1). For extinc-

tion rates up to approximately  $E = 0.1/\text{generation}$ , our results are in good agreement with the predictions of Ronce et al. (2000a). However, if  $E$  is further increased, the mean persistence time of the metapopulation declines dramatically, and none of our metapopulations persisted for 10,000 generations.

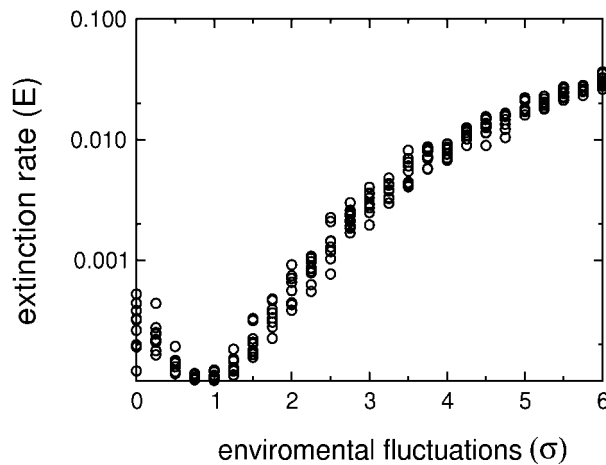
With local extinction driven by environmental fluctuations (fluctuating environment scenario;  $\epsilon = 0$ ;  $\sigma > 0$ ), the relationship between extinction rate and ES dispersal rate becomes ambiguous. We still observe the overall tendency of ES dispersal rate to increase with increasing local extinction rate ( $E$ ) and decline with increasing dispersal mortality ( $\mu$ ). However, at low extinction rates, two different ES dispersal rates may evolve for a given extinction rate (and dispersal mortality), depending on the underlying level of environmental fluctuation (fig. 2). This phenomenon is most obvious at low dispersal mortality (e.g.,

$\mu = 0.05$ ), but it vanishes when dispersal mortality becomes high (e.g.,  $\mu = 0.4$ ). We trace this surprising result to the fact that local extinction risk first declines with increasing environmental fluctuations  $\sigma$  (fig. 3). Only with a further increase in  $\sigma$  do local extinction rates start to rise as expected.

In the fluctuating environment scenario, extinction rates are not predetermined by the frequency of external catastrophes but result from fluctuations in population size. The population size is influenced by the environmentally induced fluctuations ( $\sigma$ ) in the reproductive rate ( $\Lambda$ ), by the loss of emigrating individuals (which is not very relevant for the case of density-dependent dispersal), and by the potential rescue of endangered populations due to immigration. Consequently, dispersal mortality should have an influence on local extinction rates as it affects the rescue of threatened populations. This becomes visible if we cat-



**Figure 2:** Mean evolutionarily stable dispersal rate ( $\bar{d}$ ) after 10,000 generations as a function of local extinction rate ( $E$ ) in the fluctuating environment scenario, with extinction driven by environmental fluctuations ( $0 \leq \sigma < 10$ ). Simulation runs are categorized according to dispersal mortality ( $\mu$ ). For each set of parameter combinations, the results of nine replicate simulation runs are shown. Dots on baseline indicate metapopulations that did not persist for 10,000 generations.



**Figure 3:** Effect of environmental fluctuation ( $\sigma$ ) on the emerging extinction rate ( $E$ ) in the fluctuating environment scenario, with extinction driven by environmental fluctuations. Only results for one level of dispersal mortality ( $\mu = 0.05$ ) are exemplarily shown, with nine simulation runs for each value of  $\sigma$ .

egorize the fluctuating environment experiments according to the strength of environmental fluctuations ( $\sigma$ ). At any given value of  $\sigma$ , we observe ES dispersal rates monotonously decreasing with local extinction rate (fig. 4).

We additionally tested the influence of some model assumptions concerning patch-size distribution and dispersal mode on the results of our simulation experiments. Implementing a nearest-neighbor dispersal model instead of a global dispersal model slightly altered the reducing influence of dispersal on extinction rates; consequently, there was a slightly larger extinction rate for a given dispersal rate than that shown in figures 2 and 4. This is not surprising, since patches with low population density can only be “rescued” by immigrants from occupied neighboring patches and not from any other occupied patch in the world.

Not allowing for density dependence also does not have a great effect on our results. At low environmental fluctuations ( $\sigma$ ), lower dispersal rates (approaching 0) and consequently slightly higher extinction rates emerge. However, with environmental fluctuations becoming larger, density-independent dispersal leads to slightly higher dispersal rates than our standard model.

We also ran simulations with patch capacity kept constant for all patches in the metapopulation. Here, the effect on simulation results clearly depends on the choice of patch capacity. With  $K > 30$ , demographic extinction risk becomes very small even for completely isolated patches, and thus the inverse relationship between dispersal and extinction rate visible in the lower parts of figure 2 dis-

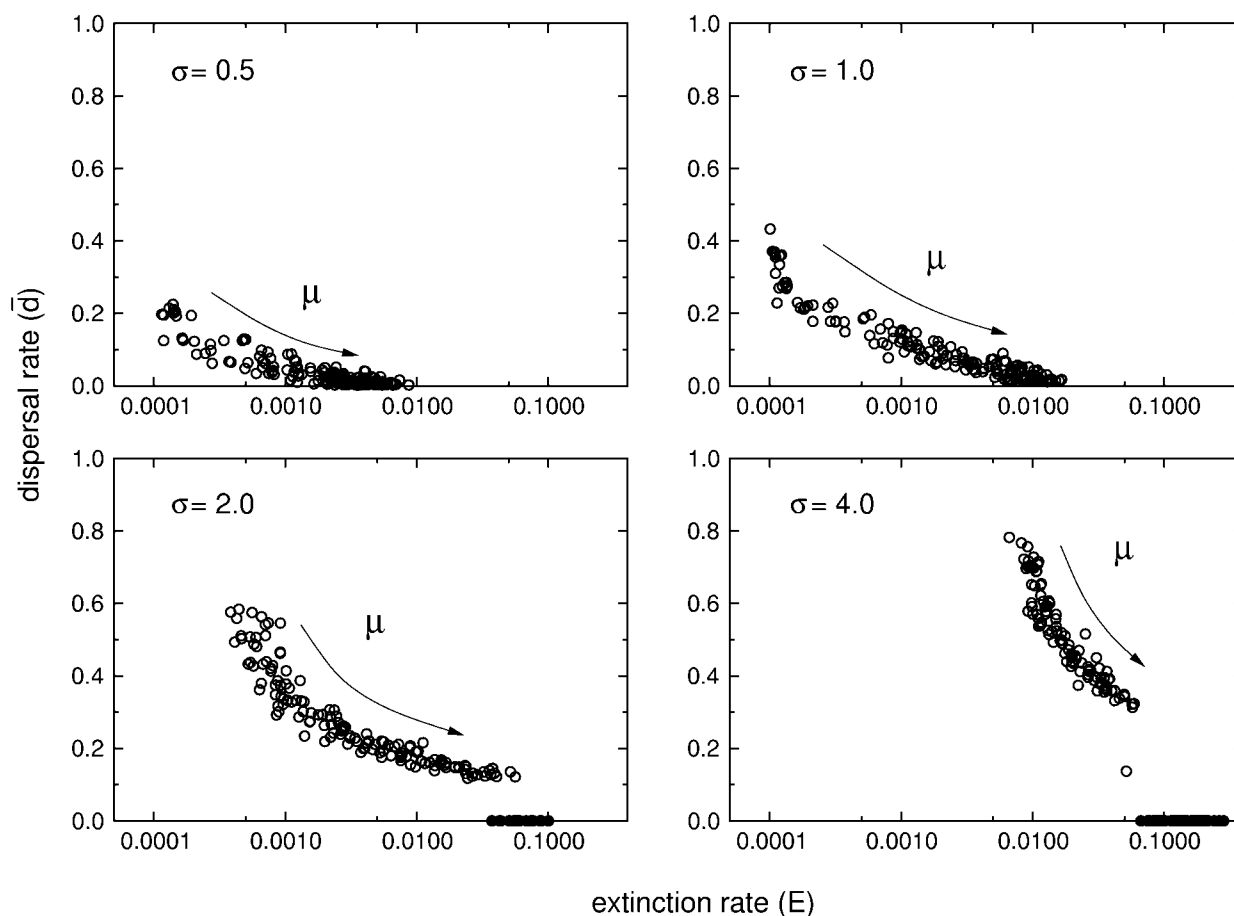
appears. For a constant patch size comparable with our standard model ( $K = 100$ ), evolving dispersal rates are generally higher, and extinction rates are somewhat lower compared with the standard model. The increase in dispersal is not surprising because spatial heterogeneity per se, as implemented in our standard model, generally selects against dispersal (cf. Hastings 1983; Holt 1985; Venable and Brown 1993; Travis and Dytham 1999).

### Discussion

The results of our simulation experiments clearly demonstrate that a general relationship between a local extinction rate and an evolutionarily stable (ES) dispersal rate does not exist. Rather, the propensity of individuals to disperse may correlate positively, negatively, or ambiguously with local extinction rates, depending on which factors cause the variance in local extinction rates.

Even though density-independent dispersal can be advantageous in an environment with spatiotemporal habitat variability (e.g., Comins et al. 1980), the benefits of dispersal will certainly be larger with a density-dependent strategy. In this case, dispersing individuals profit not only from the chance to reach an empty habitat but also from the elevated chance to reach a patch with lower population density than their current patch. Thus, a positive correlation between ES dispersal rate and variance in population size is generally predicted (Poethke and Hovestadt 2002). In our simulations, variance in population size is also positively correlated with local extinction, either because externally caused catastrophes create such variance (environmental catastrophe scenario) or because this variance leads to random extinction events (fluctuating environment scenario). Consequently, we principally expect ES dispersal rates to be positively correlated with local extinction rates.

Most authors who analyzed the relationship between local extinction rate and ES dispersal rate (e.g., van Valen 1971; Comins et al. 1980; Levin et al. 1984; Karlson and Taylor 1995; Olivieri et al. 1995; Parvinen et al. 2003; Ronce et al. 2000a) assume local extinction to be externally driven and not to be caused by random fluctuations of population size. Similar to our environmental catastrophe scenario, they create extinction events that are independent of patch capacity and population size. Ronce et al. (2000a) and Parvinen et al. (2003) have pointed out that, with very high rates ( $>0.4$ ) of externally caused extinction, local populations hardly ever reach their carrying capacity if the rates of population increase are low. Under this condition, dispersing is of little benefit, and the tendency to disperse should thus decline. Consequently, a unimodal relationship between extinction rate and dispersal rate emerged

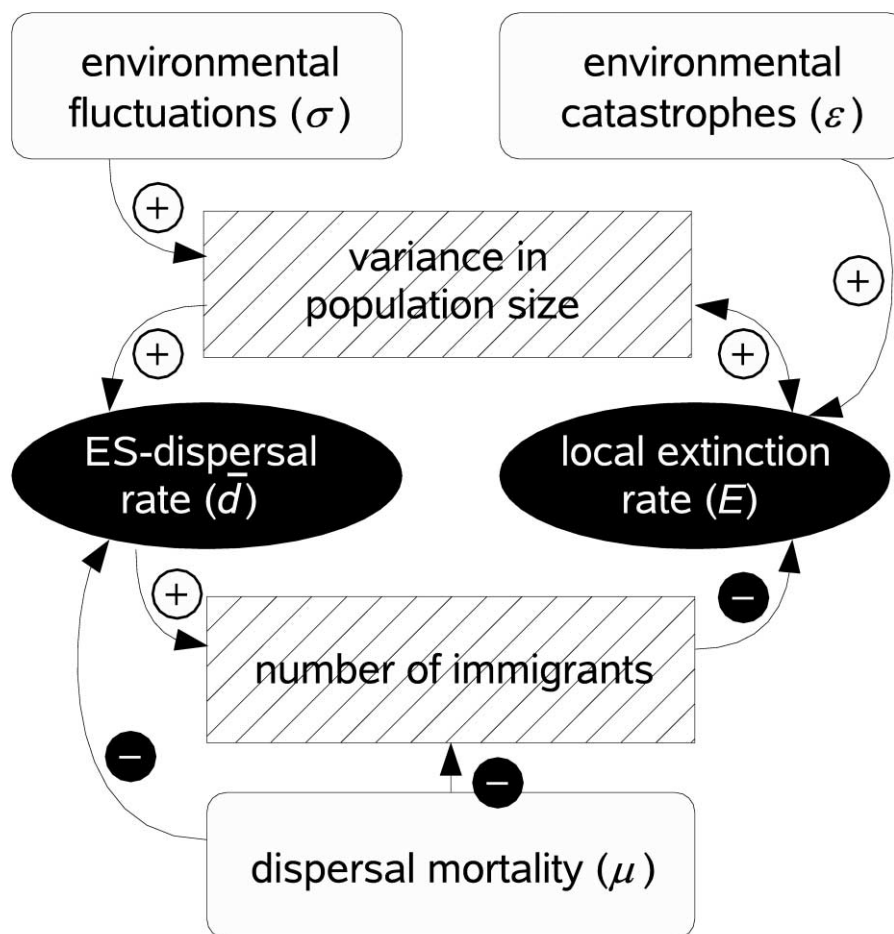


**Figure 4:** Mean evolutionarily stable dispersal rate ( $\bar{d}$ ) after 10,000 generations as a function of local extinction rate ( $E$ ) in the fluctuating environment scenario, with extinction driven by environmental fluctuations. In contrast to figure 2, simulation runs are categorized according to the intensity of environmental fluctuations ( $\sigma$ ) with dispersal mortality variable ( $0.05 \leq \mu \leq 0.9$ ) within graphs. For each set of parameter combinations, the results of nine replicate simulation runs are shown. Dots on baseline indicate metapopulations that did not persist for 10,000 generations.

in their studies. However, in our simulation experiments, we could never observe an intermediate maximum of dispersal rates simply because none of our metapopulations persisted for evolutionary time spans ( $>1,000$  generations) when extinction rates became larger than 0.1. Heino and Hanski (2001) came to a similar conclusion with a model involving a more simple mechanism (i.e., ceiling of larval density) for density-dependent regulation. Persistence of metapopulations at extremely high extinction rates becomes possible in the models by Parvinen et al. (2003) and Ronce et al. (2000a) only because they treat colonization as a deterministic process that becomes basically independent of the actual proportion of occupied patches. We thus doubt that the decline in dispersal rate at the extreme rates of external catastrophes observed in both models can ever be observed for real populations.

Even though completely externally driven population

extinctions that are independent of population size may occur in nature (e.g., Stelter et al. 1997), we do not believe them to be the rule. In most circumstances, environmental conditions may vary considerably without deterministically exterminating a population. In particular for insects, with their population dynamics strongly influenced by local weather conditions, it is appropriate to model disturbances of the environment as environmentally caused fluctuations in patch capacity or reproductive parameters. In our fluctuating environment scenario, intensity of fluctuations is implemented as variation in the number of surviving larvae per adult. In this way, we could increase extinction rates by increasing the strength of environmental fluctuations without decoupling local extinction probability from the capacity of a patch or its actual population size. A similar mechanism is incorporated in the model of Parvinen et al. (2003), who manipulated local



**Figure 5:** Schematic illustration of the factors influencing the relationship between local extinction rate and evolutionarily stable (ES) dispersal rate. The upper half of the diagram shows the positive effects of environmental catastrophes and environmental fluctuations on variation in population size. Interpatch variance in population size has an augmenting effect on both dispersal rate and extinction rate and thus leads to a positive correlation between the latter two quantities. The correlation between variability in population size and extinction rate due to environmental variation is causal. If extinctions are driven by environmental catastrophes, the correlation is due to the variance inflating effect of occasionally setting the population size to 0. The lower half of the diagram illustrates the negative effect of dispersal itself on extinction (rescue effect). This causal relationship and its dependence on dispersal mortality are responsible for an eventually emerging negative correlation between ES dispersal rate and local extinction rate.

extinction rates by changing either the frequency of catastrophes or the size of local populations and the strength of demographic fluctuations. Unfortunately, they analyzed only the effect of external catastrophes (their  $e$  is equivalent to our  $\sigma$ ) on dispersal rates but not the direct relationship between overall extinction rate and dispersal.

The positive correlation between local extinction rate and ES dispersal rate discussed in the previous paragraphs is confounded by the influence of dispersal on extinction rate. Immigrants may prevent the extinction of small populations (rescue effect). Thus, the chance of local extinc-

tion may be raised not only by increasing environmental fluctuations (or catastrophes) but also by reducing the number of immigrants. At this point, we have to recognize that dispersal mortality has a dual effect on immigration. With rising dispersal mortality ( $\mu$ ), not only do individuals become less likely to disperse due to the increasing costs of dispersal but also a smaller fraction of those dispersing will reach another habitat patch. It is thus not surprising to find the negative correlation between extinction and dispersal rate in the fluctuating environment scenarios if we keep environmental fluctuations constant (fig. 4).

An initially puzzling result of our simulations is the nonlinear relationship between the strength of environmental fluctuations ( $\sigma$ ) and extinction rate observed in the fluctuating environment scenario (fig. 3). However, according to our model, ES dispersal rates rise sharply with the strength of environmental fluctuations, especially at low levels of fluctuation and low costs of dispersal (Poethke and Hovestadt 2002). Thus, at low levels of  $\sigma$ , the extinction-promoting effect is more than compensated for by the rising number of immigrants intensifying the rescue effect (descending part in fig. 3). Only if  $\sigma$  becomes sufficiently large does the relationship become dominated by the positive influence of  $\sigma$  on local extinction rate (ascending slope of the curve in fig. 3). At this point, we have to keep in mind that ES dispersal rates will evolve to a level that maximizes individual fitness. Either increasing dispersal mortality (cost) or reducing the variability in population size (benefit) will reduce the fitness of a potential disperser. Thus, the readiness to disperse will decline, even though this may not be to the benefit of the metapopulation (cf. Comins et al. 1980).

As outlined at the end of "Results," the conclusions we draw from our model seem to be very robust against changes in model assumptions. The relationship between extinction rate and dispersal rate reported in this article is not greatly altered by the introduction of nearest-neighbor dispersal, constant patch capacity, or density-independent dispersal. The slight quantitative differences detected are in good agreement with predictions generated by existing theory.

To give a summary of our simulation results, we schematically illustrate in figure 5 the contribution of the various factors to the correlation between dispersal rate and local extinction rate. We conclude that the relationship between dispersal and local extinction rate that one may observe in field studies will strongly depend on the principal factors governing the variation in local extinction rate. First, if we compare species or populations subjected to different frequencies of environmental catastrophes, a clear positive correlation between extinction rate and dispersal rate should emerge (excluding the possibility of unrealistically high extinction rates). This could be tested by comparison of habitats with different "life expectancies." Second, when local extinction rates are due to demographic and environmentally caused fluctuations in population size, we expect to see a rise in dispersal rates with increasing fluctuations in population size. However, the correlation between dispersal rate and extinction rate may, especially at low levels of extinction, remain ambiguous even though we expect to find an overall tendency of dispersal rate to increase with extinction rate. As populations at the boundary of their distribution usually show greater fluctuations in population size as those in the center (e.g.,

Thomas et al. 1994), this situation may present an opportunity to test this hypothesis. Finally, in cases where differences in local extinction rates are primarily due to differences in dispersal mortality, we expect to observe a negative correlation between dispersal rate and extinction rate. Since patch density will influence the chance of dispersers to successfully reach a new habitat, this prediction may be validated by comparing populations of the same species in landscapes with different patch densities. Alternatively, the prediction could be tested by comparing metapopulations in landscapes that differ in the types of attributes that affect the likelihood of successful dispersal, such as patches isolated by streets, forests, or rivers versus patches that are poorly isolated.

The results of our simulation experiments suggest that the correlation between extinction rate and ES dispersal rate may not always be clear and unambiguous. As long as the relative contributions of environmental catastrophes, local population dynamic, and dispersal mortality to local extinction probability are not known, we thus recommend the use of variation in population size and dispersal mortality as predictors of ES dispersal rates.

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