The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model

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Dispersal is the process that binds the subpopulations of a metapopulation together. Previous models of the evolution of dispersal have tended to be deterministic and not spatially explicit. We develop an individual-based, spatially explicit lattice model to determine how subpopulation equilibrium density, reproductive rate and form of competition affect the rate of dispersal that is selected for. For comparison, a deterministic analogue of the individual-based model is also developed. Dispersal rate is a neutral character in the deterministic model. The individual-based model makes predictions which differ significantly from its deterministic counterpart, particularly when subpopulation equilibrium densities are low. Higher rates of dispersal evolve when reproductive rate is high and subpopulation equilibrium density is small. Our results demonstrate that the propensity to disperse is not a neutral character and that deterministic models of metapopulations should be interpreted with caution.

Keywords: dispersal, metapopulation, lattice model, evolution, patches, equilibrium density

1. INTRODUCTION

Dispersal is of vital importance in metapopulations as it is the process that binds constituent subpopulations together. Dispersal influences the long-term persistence of populations directly (e.g. Comins *et al.* 1980; Hastings 1983), the coexistence of species or genotypes (e.g. Yeaton & Bond 1991; Lavorel *et al.* 1994), and genetic differentiation between subpopulations (McPeck & Holt 1992). Understanding the process of dispersal, and the factors governing the rate at which dispersal occurs, is essential if a full and realistic picture of working metapopulations is to be achieved.

The evolution of dispersal in spatially structured populations has received considerable attention from theorists (e.g. Gadgil 1971; Hamilton & May 1977; Comins 1982; Levin *et al.* 1984; Oliveiri *et al.* 1995). Almost all models agree that temporal variation in the quality of different patches is required for dispersal to evolve (but, see Hamilton & May 1977). In a patchy environment where patch quality differs, but where the quality of a patch remains constant through time, dispersal is selected against. In a spatially and temporally constant environment dispersal is predicted to be a neutral character. In previous evolutionary models dispersal has generally been assumed to be unconditional: a fixed proportion of individuals leave a subpopulation regardless of population density or habitat quality (Hastings 1983; Holt 1985). However, McPeck & Holt (1992) and Johst & Brandl (1997) have considered the case where dispersal is conditional on habitat quality or population density respectively. When conditional dispersal strategies are modelled then dispersal may be selected for in a spatially varying but temporally constant environment (McPeck & Holt 1992). Dispersal may also be selected for in a spatially

and temporally constant environment if subpopulations have chaotic dynamics (Holt & McPeck 1996). These recent studies go some way to explaining the apparent ubiquity of dispersal across species.

Previous models investigating the evolution of dispersal tend to be deterministic and track population densities rather than individuals (but, see Comins *et al.* 1980). While such an approach may prove to be robust when subpopulation sizes are high, it is possible that it fails to make accurate predictions for the behaviour of a metapopulation comprising relatively small subpopulations. As habitats become increasingly fragmented more and more species are likely to be reduced to a number of small subpopulations linked by limited dispersal. To investigate how robust deterministic models of the evolution of dispersal might be to the stochasticity that is characteristic of such small populations, we develop an individual-based stochastic model and compare the predictions it makes with those made by its deterministic analogue.

2. THE MODEL

(a) *Model outline*

The model we develop is an extension on the two-patch model used by McPeck & Holt (1992), and a similar ten-patch model employed by Johst & Brandl (1997). For simplicity, we consider an asexual species. Genotypes differ only in their propensity to disperse: there is no trade-off between dispersal and competitive ability and dispersers suffer neither mortality during dispersal nor reduced reproductive output on arrival. The within-population dynamics consist of reproduction and competition between juveniles. Dispersal follows this competition (see figure 1).

The metapopulation is made up of $n \times n$ subpopulations inhabiting identical patches arranged on a square lattice. Such lattice models have been used previously to explore metapopulation dynamics (e.g. Comins *et al.* 1992; Dytham 1994, 1995a,b). Here we use a lattice model to explore evolution within a metapopulation. Unlike Johst & Brandl (1997) the model is spatially explicit in that dispersers move only to neighbouring subpopulations.

(b) A deterministic formulation

Within-subpopulation dynamics are carried out as follows. Assume that genotype x 's population density in the i th patch and in the t th generation is represented by $N_{x,i,t}$. Excluding mutation, the within-patch dynamics are as follows (Hassell & Comins 1976):

$$N_{x,i,t+1} = \lambda N_{x,i,t} (1 + a \sum_{x=0}^{10} N_{x,i,t})^{-b},$$

where λ is the rate of increase, and a and b relate to patch quality and the type of competition experienced by individuals, respectively. When $b=1$, the type of competition described is contest, where density dependence is exactly compensating. As b increases, the competition being described becomes increasingly scramble.

The parameter a is calculated from the following expression:

$$a = (\lambda^{1/b} - 1) / \hat{N},$$

where $\hat{N}$ is the local equilibrium density (a measure of patch quality).

When we include mutation we have, for the 11 genotype system explored in this model, the following equations:

$$N_{x,i,t+1} = \lambda[(1 - \mu)N_{x,i,t} + \mu/2(N_{x-1,i,t} + N_{x+1,i,t})] \times (1 + a \sum_{x=0}^{10} n_{x,i,t})^{-b},$$

(for $x=1, 2, \dots, 8, 9$)

$$N_{0,i,t} = \lambda[(1 - \mu/2)N_{0,i,t} + \mu/2 \times N_{1,i,t}] \times (1 + a \sum_{x=0}^{10} N_{x,i,t})^{-b},$$

$$N_{10,i,t} = \lambda[(1 - \mu/2)N_{10,i,t} + \mu/2 \times N_{9,i,t}] \times (1 + a \sum_{x=0}^{10} N_{x,i,t})^{-b},$$

where μ is the rate of mutation and λ , a , and b are the same as defined previously.

Dispersal operates between subpopulations. In the dispersal phase of the model a fraction of individuals of each genotype redistribute themselves evenly to the eight neighbouring patches, while the remainder stay behind to reproduce in their native patch. Mathematically this can be represented as follows:

$$N'_{x,i,t} = (1 - \alpha_x)N_{x,i,t} + \alpha_x N_{x,i,t}^n,$$

where $N'_{x,i,t}$ represents the post-dispersal population density of genotype x in patch i at time t , α_x is the dispersal fraction of genotype x , and is given by the following simple expression:

$$\alpha_x = x/10 \quad (\text{for } x = 0, 1, \dots, 9, 10)$$

Figure 1. The sequence of events for a subpopulation in each time step of the model.

$N_{x,i,t}^n$ is the mean predispersal population density over the eight neighbouring sites, given by:

$$N_{x,i,t}^n = \sum_{j=1}^8 N_{x,j,t}$$

where j runs over the eight nearest neighbours of patch i .

Cyclic boundary conditions are employed (opposite edges of the arena are effectively joined together creating a torus). This provides a system in which all of the cells are dynamically equivalent and is chosen to prevent any edge effects, inevitable if boundaries are reflective or absorbing, masking the other effects being investigated.

(c) An individual-based formulation

In the deterministic model it is assumed that the proportion of genotype x relative to the other genotypes, after the within-patch dynamics, is the same as it was beforehand. This is unlikely to be realistic, especially for smaller subpopulations. By chance, in a given patch, a genotype may become relatively more abundant after the within-patch dynamics than it is before them. To include this demographic stochasticity at the genotype population level we amended the model as follows: each individual present within a subpopulation at time t contributes λ offspring to a pool. This pool is reduced in size by removing individuals at random until N_{t+1} survive to make up the next generation's population. To keep the model as close as possible to the deterministic version, the same equation is used to determine how many individuals are present at $t+1$. To adapt this to an individual-based model the result is floored (you cannot have part of an individual).

An alternative approach could be taken here. The number of offspring an individual contributes to the next generation could be modelled by taking a number from a Poisson distribution with mean N_{t+1}/N_t . The main difference between this and the method adopted lies in the fact that using a Poisson distribution introduces demographic stochasticity into the subpopulation dynamics. This demographic stochasticity may affect the dispersal strategy selected for. Therefore, to allow better comparison with the deterministic model, the method described previously was chosen.

The deterministic model assumes that a fixed, genotype-dependent proportion of each genotype moves to each of the eight neighbouring subpopulations. As patch

size increases to infinity the individual-based result will approach that achieved by the deterministic formulation. In the individual-based formulation each individual has a probability of dispersal determined by its genotype. If an individual does disperse, the neighbouring site it moves to is determined at random. Similar individual-based dispersal is incorporated into models in other areas of theoretical biology (e.g. Ruxton 1996; Wilson & Hassell 1997).

3. PARAMETERS EXPLORED

(a) *Subpopulation equilibrium density (or patch size)*

The number of individuals each subpopulation is able to support may play a role in determining the rate of dispersal that is selected for. As habitat becomes increasingly degraded, patches become smaller and the equilibrium density of each subpopulation is likely to decline. To establish how changes in patch size affect the rate of dispersal selected for, the individual-based model is run using three different local equilibrium densities: 10, 20, and 50.

(b) *Reproductive rate*

The reproductive rate (λ) of individuals within subpopulations might be important in determining the rate of dispersal. To test this we apply three reproductive rates: 2, 5, and 10.

(c) *Type of competition*

The individual-based model is run for three of values of b : 1, 3, and 10. The parameter b describes the form of competition experienced by individuals within a subpopulation. When $b=1$, competition is contest (or exactly compensating), and as b increases, competition becomes increasingly scramble (or overcompensating).

(d) *Initial conditions*

For all realizations of the model the arena side length was ten ($n=10$), giving 100 patches. The lattice was initialized such that each patch has assigned to it a number of individuals equal to its equilibrium density, with each individual being selected at random to be of one of the 11 different genotypes. This selection of genotypes was not constrained to produce equal frequencies of each genotype across the entire system. For each set of parameter values the model was repeated ten times for 10 000 generations. Results were obtained by taking the mean global frequencies of each of the 11 genotypes for the final 2000 generations and then averaging over the ten runs. To allow a comparison to be made between the results provided by the individual-based and the deterministic models, the deterministic model was run using the same sets of parameter values used in runs of the individual-based model.

4. RESULTS

In a metapopulation made up of identical patches of constant quality, the deterministic model predicts that dispersal should be a neutral characteristic (figure 2). This result is independent of equilibrium density and reproductive rate and concords with results reported elsewhere (e.g.

Figure 2. Proportion of genotypes with different dispersal rates in the deterministic model (unshaded) and the individual-based model (shaded). For both the environment is spatially and temporally constant. Competition is contest ($b=1$), reproductive rate, $\lambda=2$, and subpopulation equilibrium density = 50.

Holt & McPeck 1996). The individual-based model makes contrasting predictions (figure 2). Dispersal is no longer a neutral characteristic. Individuals with an intermediate propensity to disperse occur at higher frequencies than those at the extremes.

The distribution of the dispersal genotypes depends on subpopulation carrying capacity (figure 3), reproductive rate (figure 4), and the form of competition experienced by individuals (figure 5). As subpopulation carrying capacity decreases the predicted rate of dispersal increases (figure 3). This result is in agreement with Comins (1982). As reproductive rate increases the rate of dispersal increases (figure 4). There is not such a clear relationship between the type of competition and rate of dispersal. However it appears that as the form of competition becomes increasingly scramble there is a change in the variance of dispersal rates and a slight decrease in the mean rate of dispersal.

5. SENSITIVITY ANALYSIS

The model was run using a lattice size of $n=20$, and the results obtained were consistent with those obtained for the smaller lattice employed in gaining the results shown in this paper. The results were also found to be independent of starting conditions. Rounding or ceiling (as opposed to flooring) the number of individuals in the individual-based formulation also had no observable effect on the outcome.

6. DISCUSSION

(a) *Selection for intermediate rates of dispersal*

The results show clearly that an individual-based formulation provides quite different predictions from those of the deterministic analogue. What causes the selection pressure on dispersal which is observed to occur in the individual-based model, but not in the deterministic equivalent? Probabilistic dispersal of individuals between subpopulations leads to between-patch variation in population size. Those populations which, after the dispersal phase, consist of relatively few individuals are likely to have a higher proportion of genotypes with a low propensity to disperse. This has been confirmed by the model. Conversely, a patch which has an increase in population size due to dispersal is likely to have relatively more, high propensity dispersers. The

Figure 3. The effect of subpopulation carrying capacity on the evolution of dispersal. In (a) subpopulation equilibrium density ($\hat{N}$) = 50, in (b) $\hat{N}$ = 20, and in (c) $\hat{N}$ = 10. Competition is contest ($b=1$), and reproductive rate, $\lambda=2$. For all three equilibrium densities the individual-based model is run ten times for 10 000 generations. The results shown are obtained by taking the mean proportion of each of the 11 dispersal genotypes for the final 2000 generations of each run and then averaging over the ten runs.

higher the subpopulation density is, the lower the mean fitness of individuals within the patch. Therefore dispersers incur a cost because they are more likely than non-dispersers to be in a patch which, after the dispersal-phase, is above its equilibrium density. This selects against high-dispersal genotypes.

However, very infrequent dispersal is also selected against. In the model, every individual has an equal chance of providing offspring to the next generation. By chance, all the individuals of a particular dispersal genotype may fail to reproduce successfully. That genotype then becomes extinct in the patch through genetic drift. If a low-dispersal genotype becomes extinct from a subpopulation its ability to recolonize from another patch is less than a high-dispersal genotype. In the most extreme case, of a genotype which never disperses, recolonization of a patch can only occur through mutation from one of the other dispersal genotypes. Low dispersers thus experience a cost whereby they are less efficient at recolonizing patches from which they have gone extinct.

Figure 4. The effect of reproductive rate on the evolution of dispersal. In (a) reproductive rate, $\lambda=2$, in (b) $\lambda=5$, and in (c) $\lambda=10$. For all three subpopulation equilibrium density ($\hat{N}$) = 20 and the competition is contest ($b=1$). In each case the model is run ten times for 10 000 generations. The results are obtained by taking the mean proportion of each of the 11 dispersal genotypes for the final 2000 generations of each run and averaging over the ten runs.

(b) *The effect of model parameters*

The model has mechanisms selecting against high and low propensity dispersers thus producing an increased frequency of intermediate frequency dispersal. However, our model invokes no cost for dispersal. If a cost, either in direct mortality during dispersal or in a reduction in reproductive rate for dispersing individuals, were applied it would select against dispersal. This would result in the peaks shown in figures 3–5 being shifted to the left.

Higher rates of dispersal are favoured when subpopulation equilibrium densities are low (figure 3). Decreasing the equilibrium density of subpopulations increases the intensity of selection against low-dispersal genotypes because a genotype is more likely to go extinct through the process of genetic drift within a small subpopulation than it is in a larger one. There are also fewer individuals in the metapopulation so on average it will take longer for recolonization of that subpopulation by the particular genotype to occur. However, there is also likely to be increased selection against high dispersers because when subpopulations are large the variance in subpopulation sizes following dispersal will on average be less than for smaller subpopulation equilibrium densities. As has already been

Figure 5. The effect of different forms of competition on the evolution of dispersal. In (a) $b=1$, in (b) $b=3$, and in (c) $b=10$. For all three subpopulation equilibrium density=20 and the reproductive rate, $\lambda=2$. In each case the model is run ten times for 10 000 generations. The results are obtained by taking the mean proportion of each of the 11 dispersal genotypes for the final 2000 generations of each run and averaging over the ten runs.

discussed, it is the high dispersers which are disadvantaged by this variance as they are more likely to be found in the patches which are above equilibrium density. Thus, as subpopulations become smaller, due to the stochastic nature of dispersal, the post dispersal subpopulation sizes have a higher variance and the selection against high dispersers is intensified. That higher rates of dispersal are selected for when subpopulations are smaller indicates that the increased selection pressure against low rates of dispersal outweighs any increase in selection pressure against the higher rates of dispersal. In this paper we limited ourselves to consideration of small population sizes. If subpopulations were very large we anticipate that the individual-based model's results would approach those obtained by the deterministic equivalent.

At high rates of reproduction, a higher rate of dispersal is predicted to evolve by the individual-based model (figure 4). The reason for this is that higher rates of reproduction increase the probability of a particular genotype becoming extinct from a subpopulation through genetic drift. This enhanced demographic stochasticity can be explained in the following way: consider a subpopulation with an equilibrium density of ten. At time t there are ten individuals within the subpopulation, one of which is of

genotype x . The probability of genotype x becoming extinct in the subpopulation by $t+1$ depends on the reproductive rate (see table 1). In our model, if subpopulation size at time t is $N \times t$, and there are $N_{x,t}$ individuals of genotype x , within the subpopulation, then the probability of genotype x drifting to extinction by $t+1$ is given by the following expression:

$$\frac{[\lambda(N_t - N_{x,t})]! \cdot (\lambda N_t - N_{t+1})!}{(\lambda N_t)! \cdot [(\lambda(N_t - N_{x,t})) - N_{t+1}]!}$$

where λ is the reproductive rate and N_{t+1} is the subpopulation size at time $t+1$. Thus, as reproductive rate is increased, the probability of a particular genotype becoming extinct also increases. As discussed above this extinction selects against low-dispersal genotypes. If the extinction rate increases then selection against low dispersal rate intensifies and higher dispersal strategies are favoured. This is shown in figure 4.

It is possible to argue that under certain conditions increasing reproductive rate may favour lower-dispersing genotypes. As stated previously, relatively more low dispersers are found in a subpopulation which is below equilibrium density post dispersal. When the reproductive rate is higher, lower dispersers can take full advantage of this benefit. Any trend of this nature would most likely be observed in relatively small populations and for changes between relatively low reproductive rates.

Simulations show that the form of competition experienced by individuals within a subpopulation may have a role in determining the rate of dispersal selected for. As competition becomes highly scramble ($b=10$), there is a reduced variance in dispersal rate. This result is due to intense selection against both very high and very low dispersing genotypes. With scramble competition there is an increased risk of a particular genotype becoming locally extinct as patches will frequently have few individuals occupying it. This strongly selects against low dispersers which are less likely to reinvade a patch. Scramble competition also disfavors high dispersers as they are more likely to be in patches above equilibrium density and hence suffer greater mortality.

(c) *Spatial realism*

Our model provides a framework into which greater spatial realism can be incorporated. Previous models investigating the evolution of dispersal have almost always been spatially structured, but not spatially explicit. An exception to this is the work by Comins (1982), where localized dispersal was considered. The distinction between a spatially structured and a spatially explicit approach is an important one. A spatially structured model considers the environment to consist of a number of sites linked by dispersal. Spatially explicit models form a subset of spatially structured models in which the geometry between sites is accounted for (see figure 6). While in some cases a spatially explicit model with localized dispersal may provide results which are very similar to a model in which dispersal is equally likely to all sites (e.g. Comins 1982), it will not always do so and we suspect that, as the model is made more spatially realistic, differences in results obtained through the use of a

Table 1. *The probability of a genotype going extinct by the next generation when it is represented by a single individual in a population of size ten*

reproductive rate	probability of genotype extinction	
1		=0.000
2	$18/20 \times 17/19 \times \dots \times 9/11$	=0.237
5	$45/50 \times 44/49 \times \dots \times 36/41$	=0.311
10	$90/100 \times 89/99 \times \dots \times 81/91$	=0.330
infinite	$(9/10)^{10}$	=0.349

spatially explicit, as opposed to a spatially structured, model will increase.

The distinction between a spatially explicit model and a spatially realistic model is also important. As well as considering the environment to consist of a number of sites linked by dispersal, a spatially realistic model will also incorporate spatial and temporal heterogeneity between patches. Increased spatial realism can sometimes be incorporated into spatially structured models, whether or not they are explicit. For example, through varying equilibrium densities over time and between patches (McPeck & Holt 1992).

In reality, metapopulations are not made up of a series of identical patches that remain constant in quality through time. Dispersal between patches is unlikely to be exclusively nearest-neighbour and nor will it occur with the same probability to every patch in the metapopulation (global dispersal). While a spatially structured model in which dispersal is equally likely to every patch may provide similar results to a spatially explicit model for the case when patches are spatially and temporally constant, we anticipate that the models will make differing predictions as habitat complexity increases. For example, using a spatially explicit approach will allow the effect of habitat fragmentation on the evolution of dispersal to be investigated. Different patterns of habitat loss can readily be incorporated into the model structure and the effect they have on the rate of dispersal which is predicted to evolve can be examined (see Dytham 1995*a,b*; With *et al.* 1997). The model can thus be made more spatially realistic.

The form of dispersal used in spatially explicit lattice models is almost always assumed to be nearest-neighbour. For most species this is unlikely to be particularly realistic. For example, seeds are often modelled as dispersing due to a negative exponential distribution (e.g. Okubo & Levin 1989; Portnoy & Willson 1993). The form of dispersal modelled could be made more realistic. It is possible that changing the dispersal range could effect the evolutionary outcome. The relationship between the form of dispersal modelled, the pattern of habitat loss and the rate of dispersal to evolve is an interesting area for future studies.

It would be interesting to extend the model to allow for simultaneous evolution of more than one trait and to incorporate trade-offs between different characteristics. These added complexities would both serve to increase the biological realism of the model. In this paper there is no trade-off between reproductive rate and dispersal rate.

Figure 6. Population models may be divided into two distinct sets: spatially structured and spatially unstructured. Within the set of spatially structured models exist subsets of models which are spatially explicit and introduce spatial and temporal heterogeneity. The intersect between these two subsets provides the most spatially realistic modelling alternative.

If such a trade-off had been included the mean dispersal rate would be decreased in a way similar to adding an explicit cost of dispersal, but we would expect the trends observed with changing subpopulation size, reproductive rate and the type of competition to remain largely the same.

(d) *Conclusions*

This paper extends previous studies on the evolution of dispersal by developing a spatially explicit, individual-based lattice model. The results obtained demonstrate that dispersal is not a neutral characteristic, even in a spatially and temporally constant environment. Instead selection acts against both high and low dispersing individuals causing an intermediate rate of dispersal to evolve. The precise rate that evolves depends on the equilibrium density of the patches, the reproductive rate and the form of competition. Importantly, the model we present provides a framework within which further questions can be addressed many of which, such as habitat fragmentation, can contribute to more applied fields such as conservation biology.

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