
Mixed dispersal strategies and response to disturbance

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ABSTRACT

Question: How does selection mediated by a spatially spreading disturbance affect individual-level dispersal and population-level spatial structure?

Model features: We start with a birth–death process on a lattice and introduce a spatially spreading disturbance. We consider three different scenarios affecting whether an individual recovers from disturbance, corresponding to different trade-offs between short- and long-distance dispersal.

Analytic methods: In addition to computer simulation, we use a pair approximation to conduct an invasion analysis of different dispersal strategies.

Conclusions: Of the trade-offs we examined, only a context-sensitive recovery, in which an individual's survival probability is enhanced by the presence of weaker neighbours, results in a mixed dispersal strategy.

Keywords: dispersal trade-off, invasion analysis, pair approximation, spatial disturbance.

1. INTRODUCTION

Dispersal and disturbance are significant forces in the ecological and evolutionary dynamics of a population. In this paper, we probe the interaction between the two, by investigating the conditions under which a disturbance regime selects for a mixed dispersal strategy.

The dispersal strategies available to plants are manifold, ranging from vegetative, short-range, clonal dispersal to long-distance, wind-based dispersal of seeds. Moreover, many plants adopt a mixed strategy of short- and long-distance dispersal. This can be accomplished literally, through distinct reproductive structures for two different modes of dispersal (Venable, 1985), or effectively, through seeds which fall from the parent according to a fat-tailed, or even bimodal, kernel (Nathan *et al.*, 2002).

The mix of observed dispersal strategies is mirrored in the varied costs and benefits associated with different dispersal modes. On the one hand, dispersal can benefit an individual's progeny. Indeed, offspring born of long-range dispersal may suffer less from kin competition (Hamilton and May, 1977), specialized pests (Janzen, 1970; Connell, 1971), or other deleterious effects of high density. Moreover, long-range dispersal may let a population

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exploit patches of resources which are otherwise inaccessible (Levin *et al.*, 1984). More generally, empirical observations (Friedenberg, 2003) confirm theoretical predictions (Comins *et al.*, 1980) that dispersal is a mechanism for reducing the impact of spatiotemporal uncertainty. On the other hand, we expect that long-range dispersal has associated costs, too. All else being equal, a seed with small mass disperses further than one with large mass. The reduction in mass may come at the expense of fats and other nutrients, and this deficit may degrade the viability of the seed (Nathan *et al.*, 2002). Alternatively, investment in long-distance dispersal structures may reduce the parent's viability (Cohen and Motro, 1989). Long-distance dispersal can also diminish the benefits of local adaptation, and a plant which reproduces locally may be better able to exploit local pockets of resources (Ellner and Shmida, 1981; van Groenendael *et al.*, 1997; Kisdi, 2002).

Various aspects of the trade-off between short- and long-range dispersal are addressed in the literature. The competition–colonization trade-off (Tilman, 1994; Bolker and Pacala, 1999) posits a dichotomy between (*r*-selected) species which are strong colonizers, and thus easily exploit newly available habitat, and (*K*-selected) species which outcompete the relatively transient colonizers, but are slow to expand their range. This trade-off, as well as the more mechanistic energy trade-offs sketched above, seems plausible but difficult to verify experimentally (Thompson *et al.*, 2001).

The extent of the trade-off between short- and long-range dispersal has been hypothesized to affect the evolution of dispersal strategies. Much work on the evolution of dispersal strategy has been from a purely theoretical perspective (Hamilton and May, 1977) and often uses a game-theoretic approach (Maynard Smith, 1982). Comins *et al.* (1980) and Karlson and Taylor (1992) assume that seeds far from the parent suffer from lower survival rates, and derive a predicted evolutionarily stable strategy for level of (long-distance) dispersal. While their results are somewhat contradictory (Karlson and Taylor, 1995), they find a relatively small region of parameter space in which a mixed dispersal strategy is optimal. Harada and Iwasa (1994) assume a linear trade-off between long-range dispersal and parent survival, and then calculate the strategy which maximizes population density. Harada (1999) refines this analysis, and calculates the evolutionarily stable strategy. We note that these studies impose a cost on dispersal which is essentially non-spatial; the penalty incurred due to long-distance dispersal is independent of the spatial structure of the population.

Recent work in resilience theory suggests that the spatial structure of the population may be important in the population-level response to disturbance (Thrall and Burdon, 1999; Boots *et al.*, 2004; de Aguiar *et al.*, 2004). This implies that if we want to understand the evolution of dispersal in the context of disturbance, we may need to incorporate spatial aspects into the considered costs and benefits. Modularity – that is, the organization of low-level units into well-integrated clusters, which are themselves loosely coupled – seems to be a hallmark of resilient systems (Webb and Levin, 2005). Spatial aggregation is a geometric avatar of modularity, and Webb (in preparation) has described conditions under which a mixed dispersal strategy yields a system maximally resilient to spatial disturbance. Note that this resilience is an attribute of the entire system, rather than of an individual. This sets up another potential series of trade-offs between short- and long-range dispersal in the context of disturbance with the added complication that the direct costs and benefits may occur at two different organizational levels: the individual and the population.

Disturbance has long been recognized as important in structuring ecosystems (Pickett and White, 1985), and a disturbance regime can have evolutionary, as well as ecological, con-

sequences [e.g. fire (Schwilk and Ackerly, 2001), disease (Janzen, 1970; Connell, 1971; Muller-Landau *et al.*, 2003), landslides (Guariguata, 1990; Dalling, 1994), and fluid shear (Guichard *et al.*, 2003)]. Fundamentally, disturbance can be an important source (Schippers *et al.*, 2001) of spatiotemporal uncertainty. Early work focused primarily on the rate and intensity (Pickett and White, 1985) of disturbance. More recent literature (Moloney and Levin, 1996; Ronce *et al.*, 2000; Peterson, 2002; Hiebeler, 2005; Kallimanis *et al.*, 2006) recognizes that the spatial structure of a disturbance, and not just its rate and intensity, is a significant factor in the impact of disturbance on the evolution of a population. Many disturbances are ‘contagious’ (Peterson, 2002) or otherwise spatially conditioned; from the disturbance’s viewpoint, the effect of disturbance such as fire, disease or fluid shear may be shaped by the spatial structure of the population.

Now, from the population’s viewpoint, the dispersal strategy can affect the spatial configuration of a population and ultimately the spatial spread of contagious disturbances. A population of poor dispersers shows spatial autocorrelation, while a population of long-distance dispersers tends to be uniformly distributed in space (Reed *et al.*, 2000). In this way, the dispersal strategy can potentially modulate the effect of a spreading disturbance on a population. Even recent works on the evolution of dispersal in the context of spatial disturbance (Hiebeler, 2005; Kallimanis *et al.*, 2006) do not account for this potential feedback between dispersal and disturbance.

The general principle that dispersal can mitigate the harmful effects of spatial and temporal heterogeneity in resource distribution may manifest in the evolution of dispersal strategies (Friedenberg, 2003) in response to spatially spreading disturbance. Previous work (Muller-Landau *et al.*, 2003) suggests that long-distance dispersal is advantageous both for exploiting heterogeneous resources and for avoiding the deleterious effects of spreading disturbance. In view of the relative rarity of long-distance dispersal in actual (as opposed to virtual) systems, they posit the existence of severe energetics constraints on long-distance dispersal, and using a modelling approach find evidence for the evolution of mixed dispersal strategies depending on the strength of the trade-off. However, there are clearly many potential types of dispersal trade-offs.

Our goal is to explore how the underlying dispersal trade-off affects the evolution of dispersal strategies in the context of spatially spreading disturbances. We are particularly interested in predicting the evolution of mixed dispersal strategies, because such strategies can result in spatial configurations that are more resilient to spatially spreading disturbance. This is part of the broader question of how the indirect effects of selection at the individual level may scale up to affect resilience at the population level (Williams, 1966; Webb and Levin, 2005).

In the next section, we introduce a basic spatial birth–death process and then superimpose a regime of spatially spreading disturbance. In the subsequent section, we investigate the types of trade-offs under which such a disturbance, acting as a selective agent on individuals, can give rise to the sort of mixed dispersal strategy associated with resilience. Simulations show that only certain classes of trade-offs result in a mixed strategy. We then use a mix of pair-approximation techniques and ideas from adaptive dynamics to explain these observations. Finally, we discuss our results in the context of the evolution of resilience.

2. THE MODEL

We probe these questions in the setting of a family of models in which space is discrete and time is continuous. Organisms die at rate μ and give birth at rate β . A birth event is global

with probability p , and local with probability $1 - p$. In a global birth, a site is chosen uniformly among all lattice sites. If the site is empty, it becomes occupied with the offspring of the focal individual. A local birth is similar, except that the potential birth site is chosen among the N immediate neighbours of the focal individual. We have explored this basic model elsewhere (Achter and Webb, 2006).

We model p as a quantitative trait associated with each individual, with values between 0 and 1. Concretely, we specify a mutation rate, m , and a mutation size, ε . With probability $1 - m$, $p_{\text{child}} = p_{\text{parent}}$; with probability m , $p_{\text{child}} - p_{\text{parent}}$ is drawn from a normal distribution with mean zero and variance ε . If necessary, p_{child} is truncated so that it lies between 0 and 1.

On top of this process we superimpose a disturbance, as follows. Each organism is spontaneously disturbed at rate δ , which is typically several orders of magnitude lower than μ and β . The disturbance propagates from an individual to an undisturbed individual at rate π . Finally, at rate λ the disturbance at a given site is quenched. The model is fully determined when we specify whether, or with what probability, an individual dies once the disturbance at that site has quenched.

The simulator was written in Java. The model is available as an applet elsewhere (Achter, 2006), and source code is available from the authors upon request. The simulations take place on a 300×300 grid with periodic boundaries.

3. SIMULATION RESULTS

We present four variants of our model. The first two are clearly toy models without a dispersal trade-off, and are presented solely to let us calibrate ideas. The last two impose two different trade-offs on global dispersal.

3.1. No disturbance

As a preliminary exercise, we consider the case in which $\delta = 0$, so that there is no disturbance at all.

If not all organisms are using pure global dispersal, then an individual with a higher value of p is always more fit than others. By the *fitness* of an individual we mean its (expected) number of offspring before it dies. In the absence of disturbance, all individuals experience mortality at the same rate. Therefore, instead of calculating fitness directly, we need only analyse the rate of successful birth of an individual using dispersal strategy p .

Let E_{global} be the probability that an arbitrarily chosen site on the lattice is empty, and let E_{local} be the chance that a randomly chosen neighbour of an occupied site is empty. Then the chance of a successful birth is $pE_{\text{global}} + (1 - p)E_{\text{local}}$. Both analytic methods (Achter and Webb, 2006) and simulations show that E_{global} is bigger than E_{local} , if not all individuals use pure global dispersal, while the two values are equal for pure global dispersal. Therefore, we expect – and computer simulation confirms – that the population is driven towards pure long-distance dispersal. Harada (1999) makes the same observation for a similar model.

3.2 Uniformly lethal disturbance

In the next-simplest scenario, an organism, once disturbed, inevitably dies from that disturbance. Again, the population is driven towards pure global dispersal regardless of the

strength of disturbance. On the one hand, if the quenching rate of the disturbance is high relative to its spread, then there is very little spatial correlation between disturbed sites. We expect that the analysis of the disturbance-free scenario applies. On the other hand, if the spread rate is very high relative to the quenching rate, then a disturbance removes (almost) an entire cluster from the population. Immediately after such a disturbance E_{local} is the same, while E_{global} is even larger; the population is driven towards pure global dispersal. This analysis leaves open the possibility that an intermediate ratio of quench-to-spread will favour a mixed dispersal strategy, but simulation rules this out. In fact, in simulations over a wide range of parameters, a uniformly lethal disturbance regime never selects for a mixed dispersal strategy.

Far from conferring resilience, this sometimes ensures the extinction of the entire population. For given birth and death rates (in the absence of disturbance), a higher value of p means that the steady-state population is higher, and the population tends to be more connected. There are ranges of birth and death rates for which there exists a threshold, p_{crit} ; if $p < p_{\text{crit}}$, then the population is disconnected, whereas if $p > p_{\text{crit}}$, then the population aggregates into one large cluster. In this region of parameter space, $p > p_{\text{crit}}$, a large value of p means that rapidly spreading disturbance kills off the entire population. This behaviour, also observed by Socolar *et al.* (2001), is a special case of a general phenomenon, in which maximizing fitness at the individual level leads to extinction at the level of the entire population (Webb, 2003).

3.3. Context-free trade-off

Behind many empirical and theoretical investigations of long-distance dispersal is the proposition that such dispersal is energetically costly (Rousset and Gandon, 2002; Levin *et al.*, 2003). Investment in long-distance dispersal may weaken the parent to the extent that it becomes more vulnerable to disturbance.

Now suppose that the probability that an individual recovers from disturbance is $1 - p$, so that long-distance dispersal trades off directly with the impact of the disturbance. Naïvely, we might expect that if the disturbance is a strong selective force – that is, if it is frequent and intense – then the population will ultimately stabilize at pure local dispersal, to avoid the cost associated with disturbance. Conversely, if the disturbance is quite weak, because it is rare and less intense, we might expect (as before) that the population will tend towards pure global dispersal. It is plausible that a disturbance regime of intermediate force will drive the population towards a mixed dispersal strategy.

In fact, this intuition is almost correct, and fails in a very interesting way (Fig. 1). A population subjected to a strong disturbance regime does, in fact, approach pure local dispersal; and a population subjected to a very weak disturbance regime is driven towards global dispersal. However, simulation shows that there is a distinct threshold, and that a context-free trade-off always drives the population to a pure dispersal mode. In fact, the data presented in Fig. 1 depict populations whose dispersal strategy is extreme but not literally pure. This reflects an amalgamation of finite-size effects: the population is finite; the simulation is run for a finite time; and non-trivial levels of mutation yield a small, but non-zero, number of outlying individuals. In Section 4, we use an analytic approximation of our model to explain our simulation observations.

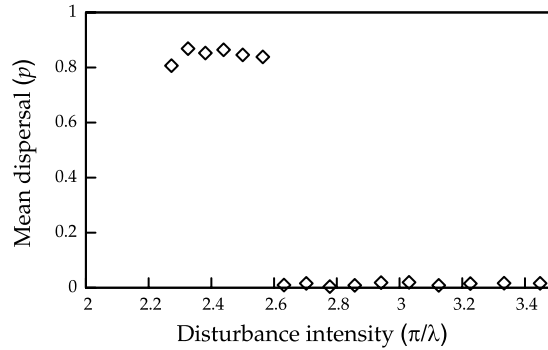


Fig. 1. The evolution of dispersal in a population subject to a context-free trade-off. The equilibrium mean value of global dispersal (p) is plotted as a function of disturbance intensity (π/λ). Parameter values: $\beta = 0.3$; $\mu = 0.05$; $\pi = 10$; $\delta = 10^{-5}$; λ varies.

3.4. Context-sensitive trade-off

Proximity of less-fit individuals may render a given individual more resistant to disturbance. For instance, certain parasites preferentially congregate on weaker hosts (Christe *et al.*, 1998; Lacroix *et al.*, 2005). In such situations, the presence of a weak individual actually improves the fitness of its neighbours. Similarly, there are assemblages of species, such as sponge colonies (Wulff, 1997), in which an individual that differs from neighbouring individuals is better able to withstand fluid shear.

Let x be a focal, disturbed organism, and define the chance that x recovers from the disturbance as

$$R = \frac{1}{N} |\{y \in \mathcal{N}(x) : y \text{ occupied and } p_y > p_x\}| \quad (1)$$

where p_x denotes the dispersal strategy used by x , $\mathcal{N}(x)$ is the set of sites adjacent to x , and $N = |\mathcal{N}(x)|$ is the size of the neighbourhood of x . In this way, the survival rate of x improves when it is surrounded by individuals that devote more resources to global dispersal.

The heuristic approach presented in the previous section still seems reasonable; a frequent, intense disturbance should push the system towards pure local dispersal, while a rare, mild disturbance should drive the population towards pure global dispersal.

Again, this is borne out, with a crucial difference. For given parameters β , μ , and δ , there exists an intermediate range of intensity which drives the system towards a mixed dispersal strategy (Fig. 2). Changing these parameters alters the location of this mixed dispersal region, but not its presence. If the chance that an organism survives a dispersal depends on its spatial context in the population, then a spreading disturbance can select for a mixed dispersal strategy. In the next section, we use an analytic approximation of our model to explain this simulation observation.

4. ANALYTICAL RESULTS

A disturbance that enforces a linear trade-off between global dispersal and disturbance survival always drives the population to a pure dispersal strategy. In contrast, a disturbance

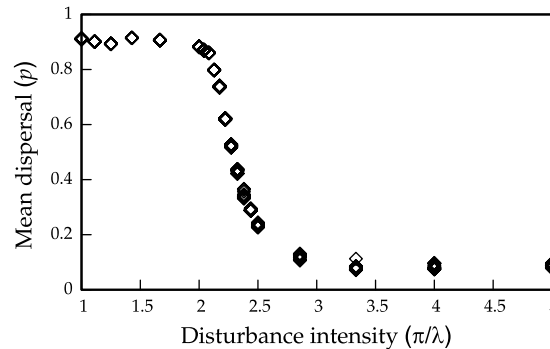


Fig. 2. The evolution of dispersal in a population subject to a context-sensitive trade-off. The equilibrium mean value of global dispersal (p) is plotted as a function of disturbance intensity (π/λ). Parameter values: $\beta = 0.3$; $\mu = 0.05$; $\pi = 10$; $\delta = 10^{-5}$; λ varies.

in which an individual's survival depends on its neighbours *can* be a selective agent for mixed dispersal strategies. A verbal argument seems insufficiently precise to distinguish between these two scenarios. We now introduce an analytic approximation of the expected behaviour of these models, and note that it enjoys good correspondence with the results from simulation. We then invoke this approximation to produce invasion plots, and thereby explain why a context-sensitive, but not a context-free, trade-off can result in selection for mixed dispersal.

4.1. Pair approximation

By accounting for pairwise interactions, but neglecting higher-order spatial correlations, we can produce a set of differential equations which captures the essential dynamics of our system. This technique has been used to model spatially explicit birth–death processes (Matsuda *et al.*, 1992; Harada and Iwasa, 1994; Achter and Webb, 2006). Recently, Hiebeler (2005) has applied this to a model which incorporates disturbance. The disturbance in Hiebeler (2005) is instantaneous, however, so that disturbed sites themselves need never be modelled.

In our model, each lattice site is either empty or occupied by a disturbed or healthy individual. We denote by $\rho(E)$, $\rho(D)$, and $\rho(H)$, respectively, the proportion of sites in each state. Let $\tau(i|j)$ denote the conditional probability that a site is in state i , given that a neighbour is in state j . In the Appendix, we show how to derive a system of differential equations to track the dynamics of the variables $\rho(i)$ and $\tau(i|j)$.

These equations model the behaviour of the system well, albeit imperfectly (Achter and Webb, 2006). In the remainder of this section, we take a game-theoretic approach and calculate the fitness of an individual in terms of these state variables. The qualitative behaviour of these fitness functions helps us explore the mechanism by which a dispersal strategy evolves.

4.2. Invasion analysis

Under the assumption of the validity of the pair approximation, we can compute the (expected) fitness $f(p_i, p_r)$ of an individual with dispersal strategy p_i ('invader') in a steady-state population of individuals with dispersal strategy p_r ('resident'). We work out a general

expression for f , and then specialize to different trade-off scenarios. Even though our approximation yields an imperfect prediction of actual steady-state values for the population, we will see that it accurately explains whether or not the disturbance can drive the population to a mixed dispersal strategy [see Harada (1999) for a closely related approach].

We emphasize that this ‘rare mutant’ analysis only applies at the beginning of an invasion, or at the initial appearance of an individual with a different phenotype from the resident population. As invader density climbs, invader–invader interactions become non-negligible, so that (Levin and Muller-Landau, 2000, p. 416) the invader may well inhibit its own spread. However, our simulation results suggest that the invasion analysis also accurately predicts outcomes once strategies reach higher frequencies.

We suppose that the population is at equilibrium, so that first-order (e.g. $\rho(H)$) and second-order (e.g. $\sigma(H, H)$) statistics are stationary. Moreover, we work under the assumption that the pair approximation holds. Now, any individual gives birth at rate β . The rate of *successful* births of an individual using strategy $p = p_i$ is

$$B := \beta \cdot (p \cdot \rho(E) + (1 - p) \cdot \tau(E|H))$$

Analysing the death rate of an individual is slightly more complicated. A healthy individual experiences a background level of mortality at rate μ . Additionally, it experiences a risk of lethal disturbance. Recall that in our model, a disturbed individual neither gives birth nor dies of background mortality. Therefore, a disturbance which results in a return to health does not contribute to the death process *or* the birth process. If we compare the process at the focal site to one in which non-lethal disturbance never happens, the expected number of progeny over the lifetime of the individual remains the same.

A healthy individual gets disturbed at rate $\delta + N \cdot \tau(D|H)\pi$; the first term measures the rate of spontaneous eruption of disturbance, while the second term measures the force of disturbance from neighbours. Given that a disturbance happens at a site, with probability R (which depends on the recovery scenario) the individual recovers, while with probability $1 - R$ the disturbance there is fatal. Therefore, the rate of *fatal* disturbance at a site is $(\delta + N \cdot \tau(D|H)\pi)(1 - R)$, and the death rate of an individual using strategy ρ is

$$\Delta := \mu + (\delta + N \cdot \tau(D|H) \cdot \pi) \cdot (1 - R)$$

Given this, the expected number of offspring of an individual before it succumbs either to background mortality or to lethal disturbance is B/Δ . Note that the resident strategy p_r intervenes in this quantity via its effect on statistics ρ , σ , and τ , while the value of $p = p_i$ affects the effective birth rate B and, possibly, the chance of recovery R .

4.3 Context-free trade-off

We apply this to the third scenario (Section 3.3), in which an individual’s chance of surviving a disturbance is $R = R(p) = 1 - p$. Given this, the expected fitness of a (rare) individual using strategy p_i in a population using strategy p_r is

$$\begin{aligned} f(p_i, p_r) &= \frac{B}{\Delta} \\ &= \frac{\beta \cdot (p_i \cdot \rho(E) + (1 - p_i) \cdot \tau(E|H))}{\mu + (d + N \cdot \tau(D|H) \cdot \pi) \cdot p_i} \end{aligned}$$

where $\rho(E)$, $\tau(E|H)$, and $\tau(D|H)$ depend on p_r as well as on model parameters. The system of equations defining the five state variables in terms of the model parameters is too unwieldy for a compact, algebraic solution. Still, we can use a mixture of algebraic and numeric techniques to analyse different strategies.

In Fig. 3, we have fixed a representative set of parameters $(\beta, \mu, \delta, \pi, \lambda)$ corresponding to a strong disturbance, and plotted the expected fitness $f(p_i, p_r)$ of an invader using dispersal strategy p_i in a population using strategy p_r . For any fixed resident strategy p_r , the optimal invader strategy is $p_i = 0$. Moreover, we see that if $p_r = 0$, then any invader with $p_i > p_r$ has a lower expected fitness than a member of the resident population. From the former observation, we expect a population with $p_r > 0$ will be successfully invaded by an individual with a lower dispersal rate. From the latter observation, we expect that $p_r = 0$ is an uninvadable strategy.

If, conversely, the disturbance is weak, a similar graph and argument predict that $p_r = 1$ is an uninvadable strategy.

In fact, even though we cannot evaluate the fitness function $f(p_i, p_r)$ directly, we can demonstrate that the resulting optimal strategy is always pure.

Note that, for a fixed set of parameters and a fixed resident dispersal strategy p_r , the fitness of an individual using strategy p_i is of the form

$$f(p_r, p_i) = \frac{a_1 p_i + a_0}{b_1 p_i + b_0}$$

Taking the derivative with respect to p , we see that this is a monotone function (either decreasing or increasing) on the interval $p = [0, 1]$. Therefore, for any resident strategy $p_r \in (0, 1)$, an invader can outcompete the resident population by adopting a pure strategy. Whether the optimal invader strategy is $p = 0$ or $p = 1$ depends on model parameters. Moreover, Fig. 3 is typical, in that the optimal invader strategy *does not* depend on the resident strategy. This means that an individual's fitness, regardless of the strategy adopted by others, is maximized at an extreme value of p .

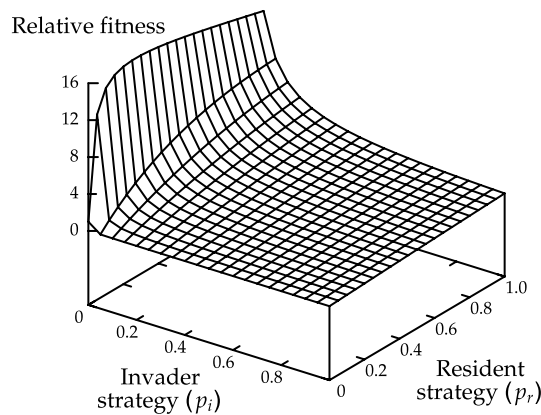


Fig. 3. The relative fitness of an invader in a homogeneous, stationary population subject to a context-free trade-off as in Section 3.4. Fitness is computed under the assumption that the pair approximation (Appendix) holds. For this set of model parameters, no matter what the resident strategy is, an invader using strategy $p = 0$ is more successful. Parameter values: $\beta = 0.3$; $\mu = 0.05$; $\pi = 10$; $\lambda = 4$; $\delta = 10^{-5}$.

This explains the thresholding seen in Fig. 1; for any set of parameters, the optimal value of p is either $p = 0$ or $p = 1$, and the population always evolves towards this evolutionarily stable strategy.

4.4. Context-sensitive trade-off

We now analyse the last scenario (Section 3.4) in a similar manner. Recall (equation 1) that an individual's chance of recovery from disturbance is proportional to the number of its neighbours which have greater probabilities of global dispersal. Combining this with Section 4.2, we see that the expected fitness of an individual using strategy p_i in a resident population using p_r is

$$f(p_i, p_r) = \begin{cases} \frac{\beta \cdot (p_i \cdot \rho(E) + (1 - p_i) \cdot \tau(E|H))}{\mu + (d + N \cdot \tau(D|H) \cdot \pi) \cdot (\tau(H|D) + \tau(D|D))} & p_i < p_r \\ \frac{\beta \cdot (p_i \cdot \rho(E) + (1 - p_i) \cdot \tau(E|H))}{\mu + (d + N \cdot \tau(D|H) \cdot \pi)} & p_i \geq p_r \end{cases}$$

The fitness function (plotted in Fig. 4) is not even continuous, let alone differentiable, so that standard techniques for analysing evolutionarily stable strategies do not immediately apply.

Still, we can at least explain why the population need not be driven to a pure dispersal strategy. In the context of a fixed resident strategy p_r , the fitness of an individual using strategy p has the form

$$f(p_r, p_i) = \begin{cases} a_1 p_i + a_0 & p_i < p_r \\ b(a_1 p_i + a_0) & p_i \geq p_r \end{cases}$$

for some b between 0 and 1.

If the population evolves strictly according to this fitness function, then a homogeneous population is never evolutionarily stable. Indeed, suppose that the resident population adopts a uniform strategy p_r . An invader using strategy $p_r - \varepsilon$ is essentially immune to the

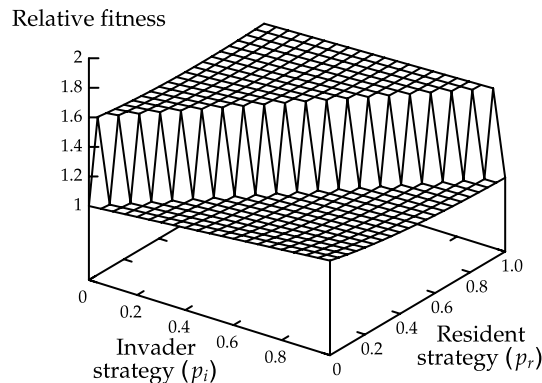


Fig. 4. The relative fitness of an invader in a homogeneous, stationary population subject to a context-sensitive trade-off as in Section 3.4. Fitness is computed under the assumption that the pair approximation (Appendix) holds. Parameter values: $\beta = 0.3$; $\mu = 0.05$; $\pi = 10$; $\lambda = 4$; $\delta = 10^{-5}$.

effects of the disturbance, while one using $p_r + \varepsilon$ reproduces more effectively but incurs no additional penalty from the disturbance. A similar argument shows that extreme values $p_r = 0$ and $p_r = 1$ are similarly vulnerable to invasion.

As noted above, this analysis is only valid at the initial appearance of a rare mutant or other invader. Still, it indicates why, as shown in Fig. 2, a context-sensitive trade-off results in a population with a mixed, rather than pure, dispersal strategy.

These findings echo those of Cohen and Levin (1991). In a somewhat different context, they find that if habitat quality is either spatially heterogeneous or temporally negatively autocorrelated, then there need not be an evolutionarily stable dispersal strategy. In some sense, spatial heterogeneity is created by the context-sensitive trade-off. The optimal strategy appears to be one which, on the one hand, can invade any other strategy, but on the other hand is invadable by other strategies as well. This is an evolutionarily compatible strategy (Cohen and Levin, 1991).

5. DISCUSSION

Perhaps not surprisingly, the predicted evolutionary outcome of selection on dispersal strategy by a spatially spreading disturbance depends heavily on the type of dispersal trade-off assumed.

Like us, Muller-Landau *et al.* (2003) investigate the evolutionary interaction between spatially spreading disturbance and dispersal strategy. Their model is quite similar to ours except that they assume a different type of dispersal trade-off. They utilize a fixed trade-off between short- and long-distance dispersal, in the form of diminished viability of seeds dispersed over long distances. Their analysis suggests, and simulations confirm, that with a fixed trade-off of this type, the population's level of long-distance dispersal converges to an evolutionarily stable strategy. Whether this strategy is pure or mixed ('intermediate') depends on model parameters.

In contrast, the dispersal trade-offs that we consider are inducible in the sense that the cost of long-distance dispersal only occurs in the context of disturbance. Of the two trade-offs considered here, the one introduced in Section 3.3 most closely parallels that of Muller-Landau *et al.* (2003). The key difference is when the cost of dispersal is incurred. In Muller-Landau *et al.* (2003), the offspring of a long-distance disperser always suffer from diminished viability; the presence of infection may actually confer an evolutionary benefit to long-distance dispersers, since their offspring may escape pockets of infection. In contrast, in Section 3.3 a long-distance disperser is penalized only when it becomes disturbed.

In Muller-Landau *et al.* (2003), the cost associated with dispersal occurs regardless of disturbance. The level of dispersal favoured may be correlated with resilience but, if so, this is an exaptation. With our model, the indirect effects of dispersal strategy on disturbance structure feed back on individuals. Selection at the individual level could lead to higher-level patterns which increase resilience, since the same selective agent is important at both levels.

When the trade-off is fixed with regard to disturbance, predicting the equilibrium strategy is tantamount to solving an optimization problem. In contrast, in the models studied here, the underlying adaptive landscape changes as the population evolves. In such generality, diverse evolutionary outcomes are possible, including evolutionarily stable strategies, evolutionarily compatible strategies, or co-existence of multiple stable strategies. Levin and Muller-Landau (2000) present a lucid taxonomy of the possibilities for stability, and provide a clear theoretical account of the evolutionary stability of dispersal strategies in a wide range

of contexts. Unfortunately, the methods of Levin and Muller-Landau (2000) do not apply directly to the model of Section 3.4, because the fitness function is not continuous.

Clearly, the evolution of mixed dispersal strategies is possible with different types of trade-offs. This evolution of mixed dispersal strategy suggests that the evolution of spatial modularity via individual-level selection may be possible despite spatial structure being a population-level property. The next step in understanding the evolution of resilience is to determine quantitatively whether the level of spatial modularity that evolves is sufficient to enhance the resilience of the population to spatially spreading disturbance.

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APPENDIX: THE PAIR APPROXIMATION

As in Section 4.1, let $\rho(i)$ be the proportion of sites in state i , and let $\tau(i|j)$ be the conditional probability that a site is in state i , given that a neighbour is in state j . Let $\sigma(ij)$ denote the proportion of neighbouring sites (x_1, x_2) which are either in states (i, j) or (j, i) . (Thus, a pair of sites (H, E) contributes to $\delta(HE)$, as does a pair of sites (E, H) .)

In the pair approximation (Harada and Iwasa, 1994; Achter and Webb, 2006), higher-order correlations are ignored so that, for instance, $\tau(i|jk) = \tau(i|j)$. Under this assumption, we can write down equations for the dynamics of these state variables as functions of time. The method, while lengthy, is straightforward. We enumerate all event types and the rates at which they happen. Then, for each event, we calculate its effect on each of the state variables.

At the end of this Appendix, we carry out this program. Before doing so, however, we make some remarks on how to reduce the apparent complexity of the resulting system of equations.

In fact, all state variables can be rewritten in terms of $\rho(H)$, $\rho(D)$, $\sigma(HH)$, $\sigma(HD)$, and $\sigma(DD)$.

First, any reference to $\rho(E)$ can be eliminated, as

$$\rho(H) + \rho(D) + \rho(E) = 1.$$

Second, we can eliminate variables of the form $\tau(E|*)$, using

$$\tau(H|*) + \tau(D|*) + \tau(E|*) = 1.$$

Finally, we can rewrite τ in terms of σ . The only intricacy is to account for symmetries of pairs. By the usual calculus of conditional probabilities, we have

$$\sigma(ii) = \tau(i|i)\rho(i);$$

the chance that two neighbouring sites are both in state i is the chance that one of the sites is in state i times the conditional probability that the other is in state i , *given* that its neighbour is in state i .

Now suppose that $i \neq j$ are two distinct states. Then – recall that there are *two* different ways to get a pair which counts towards $\sigma(ij)$ –

$$\sigma(ij) = \tau(i|j)\rho(j) + \tau(j|i)\rho(i).$$

We assume that there is no directional bias, so

$$\tau(i|j)\rho(j) = \tau(j|i)\rho(i)$$

whence

$$\sigma(ij) = 2\tau(ij)\rho(j).$$

Applying these substitutions gives a closed system of partial differential equations in the variables $\rho(H)(t)$, $\rho(D)(t)$, $\sigma(HH)(t)$, $\sigma(HD)(t)$, and $\sigma(DD)(t)$. We note that in the absence of disturbance, so that $\delta = \pi = \lambda = 0$, these equations reduce to those of Achter and Webb (2006) and Harada and Iwasa (1994).

For the derivation itself, note that there are five kinds of events: death, birth, (spontaneous) disturbance, propagation, and quenching. We briefly analyse the rate and effect of each type of event.

- (1) *Death*. Death happens at rate $\mu\rho(H)$. Thus, at rate $\mu\rho(H)$, sites in state $\rho(H)$ change to state $\rho(E)$. We summarize this transition with the diagram

$$\rho(H) \xrightarrow{\mu\rho(H)} \rho(E)$$

Moreover, each death affects the neighbours of the site. For each state $*$, the expected number of neighbours of the focal site in state $*$ is $N\tau(*|H)$. Therefore, for $* \in \{H, D, E\}$, we have

$$\sigma(*H) \xrightarrow{\mu\rho(H)N\tau(*|H)} \sigma(*E)$$

- (2) *Birth*. A healthy individual gives birth at rate β . With probability p , this is a global birth. With probability $1 - p$, the birth is local.

- (a) *Global birth*. Global births happen at rate $\beta\rho(H)p\rho(E)$, as we must multiply by the probability that the target site is actually empty.

$$\rho(E) \xrightarrow{\beta\rho(H)p\rho(E)} \rho(H)$$

The effect on neighbouring sites is:

$$\sigma(*E) \xrightarrow{\beta\rho(H)p\rho(E)N\tau(*|E)} \sigma(*H)$$

- (b) *Local birth*. Local births happen at rate $\beta\rho(H)(1-p)\tau(E|H)$.

$$\rho(E) \xrightarrow{\beta\rho(H)(1-p)\tau(E|H)} \rho(H)$$

At the very least, this increases the number of HH pairs by one:

$$\sigma(H E) \xrightarrow{\beta \rho(H)(1-p)\tau(E|H)} \sigma(H H)$$

We use the pair approximation to calculate the effect on other neighbours of the new progeny:

$$\sigma(* E) \xrightarrow{\beta \rho(H)(1-p)\tau(EH)(N-1)\tau(*|E)} \sigma(* H)$$

(3) *Disturbance*. Disturbance erupts spontaneously at rate $\delta \rho(H)$, yielding the transition

$$\rho(H) \xrightarrow{\delta \rho(H)} \rho(D)$$

The effect on neighbours is summarized by:

$$\sigma(* H) \xrightarrow{d \rho(H) N \tau(*|H)} \sigma(* D)$$

(4) *Propagate*. Disturbance propagates (successfully) at rate $\pi \rho(D) \tau(H|D)$. The analysis is much like that of the local birth process.

$$\rho(H) \xrightarrow{\pi \rho(D) \tau(H|D)} \rho(D)$$

$$\sigma(D H) \xrightarrow{\pi \rho(D) \tau(H|D)} \sigma(D D)$$

$$\sigma(* H) \xrightarrow{\pi \rho(D) \tau(H|D)(N-1)\tau(*H)} \sigma(* D)$$

(5) *Quench*. The disturbance quenches at rate $\lambda \rho(D)$. Depending on the recovery scenario, the individual may recover or die.

(a) *Quench and recover*. This happens at rate $\lambda \rho(D) R$.

$$\rho(D) \xrightarrow{\lambda \rho(D) R} \rho(H)$$

$$\sigma(* D) \xrightarrow{\lambda \rho(D) R N \tau(*|D)} \sigma(* H)$$

(b) *Quench and die*. This happens at rate $\lambda \rho(D) (1 - R)$.

$$\rho(D) \xrightarrow{\lambda \rho(D) (1 - R)} \rho(E)$$

$$\sigma(* D) \xrightarrow{\lambda \rho(D) (1 - R) N \tau(*|D)} \sigma(* E)$$