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LETTER

Multiple risk reduction mechanisms: can dormancy substitute for dispersal?

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Abstract

In a spatiotemporally variable environment, plants use seed dispersal and dormancy to reduce risk. Intuition suggests that dormancy should be able to substitute for dispersal, so that dormancy will reduce the optimal mean dispersal distance, and previous theoretical studies using temporally uncorrelated environments have found this to be true. I show that in the presence of positive temporal correlations, dormancy instead increases dispersal: dormancy and dispersal are not interchangeable risk reduction mechanisms. Dispersal has both costs (seeds landing in unfavourable habitat) and benefits (seeds being in place to exploit newly favourable habitat). I discuss how the costs and benefits balance to determine optimal dispersal and how dormancy shifts this balance, causing dispersal to increase. I also find that an interaction between spatial and temporal correlations determines whether an evolutionarily stable dispersal distance exists at all and confirm the expectation that increasing the scale of spatial correlations causes dispersal to increase.

Keywords

Branching point, dispersal, dormancy, environmental variation, evolution, germination, spatiotemporal, tradeoff.

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INTRODUCTION

Environmental conditions vary in both space and time. Among the ways plants cope with this uncertainty are seed dispersal, which spreads offspring across multiple locations, and seed dormancy, which spreads seeds across multiple years. Intuitively, we expect the presence of one risk reduction strategy to reduce the need for the other: dormancy, sometimes called dispersal in time, should be able to substitute for dispersal in space. In apparent confirmation, several theoretical studies using temporally uncorrelated environments have shown that if dormancy is increased, the optimal fraction of offspring that disperse becomes smaller, so that the optimal mean dispersal distance is shorter (Venable & Lawlor 1980; Bulmer 1984; Levin *et al.* 1984; Klinkhamer *et al.* 1987; Cohen & Levin 1991).

In an environment with positively autocorrelated temporal fluctuations, however, this need not be the case. This fact was first hinted by Cohen and Levin, who used a model in which the environment took one of two possible values each year. A fraction of the seeds were distributed uniformly among all the habitat patches, which had no explicit spatial configuration, and the rest of the seeds remained in their natal patch. The researchers noted briefly that in environments with a positive correlation between successive years, it is possible for dormancy to increase the optimal dispersal fraction (Cohen & Levin 1991). In this study, I use a fully spatial model. The environment varies randomly and is positively correlated in space and time. I assume that offspring dispersal distance is exponentially distributed, a common assumption for wind-borne seeds (Kot *et al.* 1996), and find the optimal mean dispersal distance with and without dormancy as a function of the distances and time intervals over which the environment is correlated. Where an evolutionarily stable state (ESS) exists, I find that dormancy increases the optimal mean dispersal distance. Dispersal has both costs (seeds landing in unfavourable habitat) and benefits (seeds being in place to exploit newly favourable habitat). By reducing the responsiveness of the population to newly favourable habitat, dormancy reduces the benefit of dispersal. However, dormancy also reduces the number of seeds landing in unfavourable habitat and thereby reduces the cost of dispersal. The reduction in cost outweighs the reduction in benefit, so that dispersal distance increases. This implies that, far from being substitutible, dispersal in time may actually interfere with dispersal in space. If we observe that shorter dispersal distances are associated with higher dormancy, as is naively expected, then we cannot infer that dispersal and dormancy can be substituted for each other but must instead seek some other explanation.

I also find that when the environment is sufficiently unpredictable (correlated only over short time intervals), branching points take the place of ESSs, so that the population becomes polymorphic. Increasing the scale of spatial correlations causes the transition from ESS to branching point to occur at higher levels of environmental predictability (correlated over longer time intervals). Dormancy increases the branching point dispersal distance just as it increases the ESS dispersal distance. Finding the optimal dispersal distances in the polymorphism is beyond the scope of this paper. As an approximation, however, I investigate all-or-nothing dispersal, in which a fraction of the seeds disperse globally and the rest do not disperse. I find that dormancy reduces the optimal fraction of dispersers when the environment is correlated only over short time intervals and increases the optimal dispersal fraction when the environment is correlated over longer time intervals. This suggests that the traditional dormancy–dispersal tradeoff may hold if the environment is correlated over a sufficiently short time scale and if, instead of optimal dispersal distance, we consider the proportion of far-dispersing seeds in a dispersal polymorphism.

MODEL AND ANALYSIS

Consider the following annual plant model in discrete time and space. (A similar model is discussed in greater detail in Snyder & Chesson (2004)). Seeds at location x at time t germinate with probability G and upon establishing themselves as adult plants produce a maximum number of seeds $F(x, t)$ (fecundity). Fecundity varies across space and time as a result of local environmental conditions. As a reminder of this, I refer to fecundity as the environmental response, or simply 'the environment' for short. However, most individuals will produce fewer than $F(x, t)$ seeds. Seed production is reduced by competition, C, which is determined by a weighted average of the local seedling population, with weight function U defined so that more distant seedlings have less of a competitive effect ($U(z) = 1/(2b)e^{-|z|/b}$). Seeds disperse; the dispersal kernel $k(z)$, with mean dispersal distance a, gives the probability that a seed will travel a distance z from its parent. Seeds that do not germinate survive until the following year with probability s. The density of seeds at location x in year $t + 1$ is then given by

$$n(x, t+1) = \sum_{y=-\infty}^{\infty} k(x-y)\lambda_1(y,t)n(y,t) + \lambda_2(x,t)n(x,t), \qquad (1)$$

where $\lambda_1(x, t)$, the per capita contribution of germinating seeds to next year's seed bank, is given by

$$\lambda_1(x,t) = \frac{F(x,t)G}{C(x,t)}, \qquad (2)$$

$\lambda_2(x, t)$, the per capita contribution of non-germinating seeds to next year's seed bank, is given by

$$\lambda_2(x,t) = s(1-G) \qquad (3)$$

and competition $C(x, t)$ is given by

$$C(x,t) = \sum_{y=-\infty}^{\infty} U(x-y)Gn(y,t). \qquad (4)$$

Dormancy, D, depends on both germination and seed survival probabilities and can be thought of as the probability that a seed fails to germinate and survives until the next year: $D = s(1 - G)$. For a given pattern of environmental variation, the optimal dispersal distance depends only on D and not on s or G independently. (That is, changes to either s or G result in changes to D, and it is the value of this compound parameter which determines the effect on dispersal.)

The environment varies randomly but is positively correlated in space and time. The correlation between fecundity values at the same time falls off exponentially with their spatial separation, the exponential characterized by spatial correlation length ξ. Similarly, the correlation between fecundity values at the same location falls off exponentially with their separation in time, the exponential characterized by temporal correlation length τ. Thus,

$$\mathrm{Corr}(F(x'+x, t'+t), F(x', t')) = \exp\left(\frac{-|x|}{\xi}\right)\exp\left(\frac{-|t|}{\tau}\right). \qquad (5)$$

Environmental conditions are similar over a distance roughly equal to the spatial correlation length ξ and over a time roughly equal to the temporal correlation length τ. One can therefore think of a larger ξ as indicating a system with a larger 'patch size', and a larger τ as indicating a more predictable environment.

To find the optimal dispersal distance for environmental variation at a given spatial and temporal scale, consider a resident community with mean dispersal distance a_r and a rare mutant type (the 'invader') with mean dispersal distance a_i. (By rare, I mean that the contribution of mutants to competition is negligible.) The invader population will increase as long as its regional growth rate (the growth rate of the spatially averaged population) is positive. However, in a time-varying environment, a population's ultimate fate is determined by its long-run growth rate $\bar{r}_i$, defined as the geometric average of the yearly growth rate (Lewontin & Cohen 1969). For a mean resident dispersal distance a_r, the invader's optimal dispersal distance a_i is found by maximizing its long-run regional growth rate:

$$\frac{\partial \bar{r}_i(a_i, a_r)}{\partial a_i} = 0. \tag{6}$$

At equilibrium (Nash equilibrium), the invader can do no better than to adopt the response of the resident, and so the optimal dispersal distance a^* is found by solving

$$\left.\frac{\partial \bar{r}_i(a_i, a_r)}{\partial a_i}\right|_{a_i=a_r=a^*} = 0 \tag{7}$$

and checking to see that this is a maximum (Rice 2004, ch. 9). If a^* is the unique best strategy (i.e. there are no ties), then the Nash equilibrium is an ESS. All Nash equilibria in this study are ESSs.

To relate $\bar{r}_i$ to the local growth rate $\lambda_i(x, t) \equiv \lambda_{1i}(x, t) + \lambda_{2i}(x, t)$, we must first find the regional growth rate. Let us denote spatial averages by $\langle\cdot\rangle_x$ and time averages by $\langle\cdot\rangle_t$. As shown in Chesson (2000), the spatially averaged population $\langle n\rangle_x(t)$ has dynamics $\langle n\rangle_x(t+1) = \tilde{\lambda}(t)\langle n\rangle_x(t)$, where the regional growth rate $\tilde{\lambda}(t)$ equals $\langle\lambda\rangle_x(t) + \mathrm{Cov}(\lambda, v)_x(t)$, $v(x, t) = n(x, t)/\langle n\rangle_x$, and $\mathrm{Cov}(f, g)_x(t)$ is the spatial covariance of f and g at time t. We finish by taking the geometric average of the regional growth rate to find the long-run regional growth rate: $\bar{r}_i = \langle \ln \tilde{\lambda}_i(t)\rangle_t$. Because the invader does not contribute to competition, λ_i does not depend on the invader's population distribution and thus does not depend on a_i. Therefore, we can find the optimal dispersal distance by (numerically) solving

$$\left.\frac{\partial \bar{r}_i(a_i, a_r)}{\partial a_i}\right|_{a_i=a_r=a^*} = \left.\frac{\partial}{\partial a_i}\langle \mathrm{Cov}(\lambda_i, v_i)_x\rangle_t\right|_{a_i=a_r=a^*} = 0. \tag{8}$$

An approximate expression for $\langle \mathrm{Cov}(\lambda_i, v_i)_x\rangle_t$, valid when environmental variation is not too large, is derived in Appendix S1.

RESULTS

Evolutionarily stable strategies

Consider first dispersal without dormancy. Figure 1 shows that the optimal dispersal distance increases as the environment is correlated on a shorter time scale or a longer spatial scale. This accords with our intuition. If the temporal correlation length is long, offspring born in a favourable location are likely to continue to enjoy favourable conditions if they disperse short distances and remain close to their natal site, although the benefit of favourable environmental conditions must be weighed against the negative consequences of increased competition. Because favourable areas have higher local growth rates and produce the most offspring, short-range dispersal causes the population to accumulate in the favourable areas, and the regional scale and long-run regional scale growth rates are increased (Pacala & Roughgarden 1982; Snyder & Chesson 2003; Abrams & Wilson 2004). When the temporal correlation length is short, current favourability is no guarantee of future favourability, so retaining offspring locally is risky. Instead, long-range dispersal ensures that some offspring will land in a new favourable location (Gadgil 1971; Levin *et al.* 1984; Travis 2001). Spatial scale also affects dispersal distance. When the environment is correlated over larger distances, then an individual in an unfavourable environment will have to send its seeds farther away to find better conditions (Palmer & Strathmann 1981; Travis 2001).

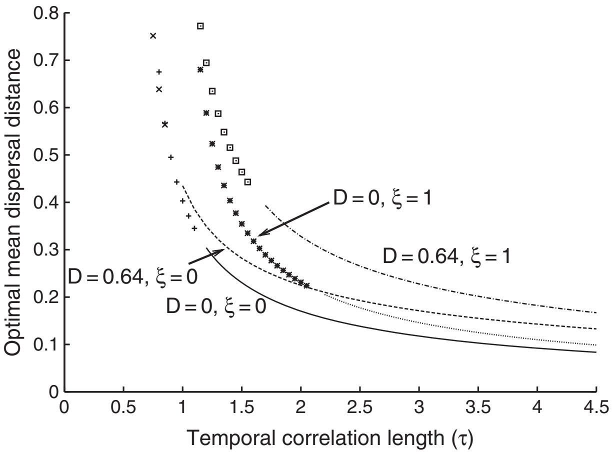

Figure 1 Optimal mean dispersal distance vs. the temporal correlation length (τ) for different dormancies (D) and different spatial correlation lengths (ξ). Increasing ξ or decreasing τ increases the optimal mean dispersal distance. Increasing dormancy reduces the optimal mean dispersal distance. The continuous lines represent evolutionarily stable states (ESSs) while the symbols represent branching points. Increasing the spatial correlation length causes the transition from branching points to ESSs to occur at a larger temporal correlation length. In all the figures, the competition parameter b is 1, the mean fecundity $\langle F\rangle_{x,t}$ is 5 and $\mathrm{var}(F) = 0.25$.

It is reassuring to see our intuitions about dispersal distance confirmed, but precisely how is the optimal dispersal distance determined? The mathematical prescription given in eqn 8 is worked through in the online supplement. The mathematical expressions derived there can be interpreted as stating that dispersal has two effects on populations: it distributes the population more evenly in space, smearing the population distribution, and it reduces the delay between environmental change and the population's local response, since as offspring disperse more widely, they are more likely to be in place to take advantage of newly favourable habitat. Reducing the response delay is always advantageous. Whether the extra smearing that comes from increasing dispersal is advantageous depends on how rapidly the environment is varying. Consider first sinusoidal variation in space and time: $E(x, t) = B \sin(qx) \sin(\omega t)$. Because this year's population tends to be concentrated wherever growth was highest last year, the population often ends up concentrated in suddenly unfavourable locations when the environment is changing rapidly. The population density at location x at time t is $n(x, t) = B' \sin(qx) \sin(\omega t + \psi(q, \omega))$, where the delay, measured as an angle or 'phase shift' ψ, is at its largest magnitude. (The population is nearly '180° out-of-phase' with the environment.) In such a case, the additional smearing produced by increasing dispersal confers a benefit because it reduces the population's concentration in unfavourable areas. However, when the environment is changing slowly, this year's environment is much like last year's, so that the population is concentrated in favourable areas. In this case, the additional smearing produced by increasing dispersal is disadvantageous.

The environment does not vary sinusoidally, of course, but instead inevitably varies at multiple time scales. For example, slower variation due to the El Niño/Southern Oscillation cycle may be superimposed on more rapid year-to-year variation. The temporal correlation length τ tells us the balance of fast and slow variation. When τ is large, the environment is predictable for a long time and almost all of the temporal variation is slow. When τ is small, the environment is predictable for only a short time and a larger proportion of the variation is fast, although there is still slow variation present (Fig. 2a).

The optimal dispersal distance is the distance at which the cost and benefit of increasing dispersal precisely balance, so that any further increase in dispersal would produce a net cost. The temporal correlation length (τ) helps to determine the relative magnitudes of the cost and benefit. When τ is large and most variation is slow, the smearing effect of dispersal is a cost and the delay reduction effect is a benefit. The two balance at a relatively low mean dispersal distance. When τ is small, most of the variation is rapid, where dispersal's smearing effect becomes a benefit. This shift

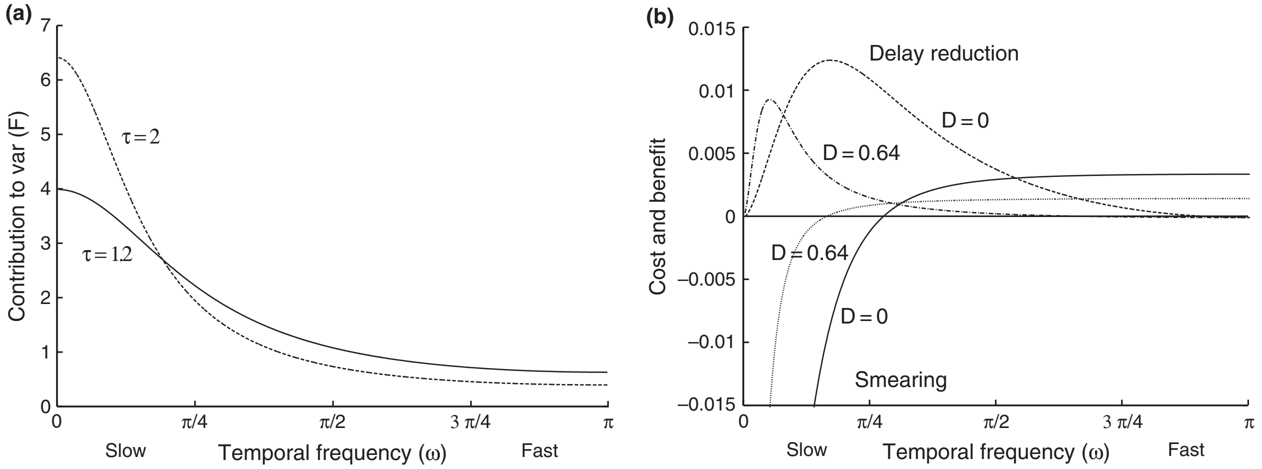

Figure 2 (a) The amount of environmental variation present at different time scales for two values of the temporal correlation length. This plot shows the contribution to $\mathrm{Var}(F)$ from environmental variation at different temporal frequencies. Summing the variation present at all frequencies yields $\mathrm{Var}(F)/\langle F\rangle^2_{x,t}$. (In the notation of the online supplement, this plot shows the spectral density of the environmental variation, $|\tilde{\epsilon}|^2(q, \omega)$, integrated over q.) Frequency = 2π/period, and so a small frequency represents slow variation while a large frequency represents fast variation. The environment with the larger temporal correlation length is more predictable and is composed of a greater proportion of slow variation. For both (a) and (b), the spatial correlation length $\xi = 0.001$. (b) Costs and benefits of increasing dispersal for variation at different temporal frequencies. Negative values represent costs and positive values represent benefits. Resident and invader dispersal distances are set equal to the evolutionarily stable state value. The solid and dotted lines show the smearing effect of dispersal with no dormancy and with $D = 0.64$ respectively. (In the notation of the online supplement, the lines show the integral over q of $(\partial G/\partial a_i)(q, \omega) \cos \psi(q, \omega)[1 + \tilde{U}^2(q)R^2(q, \omega) - 2\tilde{U}(q)R(q, \omega)\cos \phi(q, \omega)]$, where a_i is the mean dispersal distance.) Dormancy reduces both the costs and the benefits of smearing. The dashed and dash-dotted lines show the delay reduction effect of dispersal with no dormancy and with $D = 0.64$ respectively. (In the notation of the online supplement, the lines show the integral over q of $-G(q, \omega) \sin \psi(q, \omega)(\partial\psi/\partial a_i)(q, \omega)[1 + \tilde{U}^2(q)R^2(q, \omega) - 2\tilde{U}(q)R(q, \omega) \cos \phi(q, \omega)]$). Dormancy reduces the benefit of delay reduction at all but the smallest frequencies. The total contribution of either smearing or delay reduction to $(\partial/\partial a_i)\langle \mathrm{Cov}(\lambda_i, \nu_i)_x\rangle_t$ is found by multiplying the value shown here by the amount of environmental variation present at the same frequency (part a) and summing over frequency.

from cost to benefit reduces the overall cost of dispersal, and the optimal mean dispersal distance increases. Figure 2b shows the contribution of the smearing and delay-reducing effects of increasing dispersal as a function of the time scales of the variation present in the environment. Where an effect is negative, it is a cost, and where it is positive, it is a benefit. The total contribution of either effect is found by multiplying the contribution of the effect at a given time scale by the amount of environmental variation present at that time scale and summing over time scales. Adding the total contributions of smearing and delay reduction gives $\frac{\partial}{\partial a_i}\langle \mathrm{Cov}(\lambda_i, \nu_i)_x \rangle_t \big|_{a_i=a_r=a^*}$. The optimality condition, eqn 8, sets this expression equal to zero and thus states that at the optimal mean dispersal distance, the costs and benefits of increasing dispersal precisely balance.

Dormancy changes the cost and benefit of increasing dispersal, shifting the balance point. Dormancy reduces smearing because a smaller proportion of the offspring disperses. This reduces the cost of smearing when the environment is changing slowly and reduces the benefit of smearing when the environment is changing rapidly. Dormancy also causes the current population distribution to depend on seed production from increasingly long ago, making the population less responsive to the current environment and increasing the response delay ψ. The delay still decreases as dispersal distance increases, but it does not decrease as much and takes longer to reach its limiting value (Fig. 3). The net result is that the benefit produced by dispersal is reduced over all but the slowest scales of variation. Figure 2b shows how the smearing and delay-reducing effects of increasing dispersal change when dormancy is introduced.

The net result is that in an environment with positive temporal correlations, dormancy increases the ESS dispersal distance (Fig. 1). Figure 2 shows that even for relatively unpredictable environments (small τ), much of the variation is at the longest scales, where dormancy reduces the cost of dispersal and increases the benefit. There is also plenty of variation at intermediate time scales, where dormancy reduces the benefit from delay reduction. This reduced benefit, however, is more than compensated for by the reduced cost of smearing. There is relatively little variation at the shortest time scales, where dormancy reduces the benefit of both smearing and delay reduction. The smaller τ is, however, the more variation there is at short time scales, and the less dormancy increases dispersal.

In other words, in an environment with some degree of predictability ($\tau > 0$), the natal location has a greater than random probability of being favourable again next year, as opposed to locations significantly farther away than the spatial correlation length, about which nothing can be predicted. Dispersal into these unpredictable areas is therefore costly. By spreading out the germination times of seeds that may have landed in currently unfavourable areas, dormancy reduces this cost, and this benefit outweighs the cost of delaying the germination of seeds that have, in fact, landed in currently favourable habitat. The less predictable the environment is, however, the less dispersing is any worse than staying in place, and the less benefit dormancy can provide.

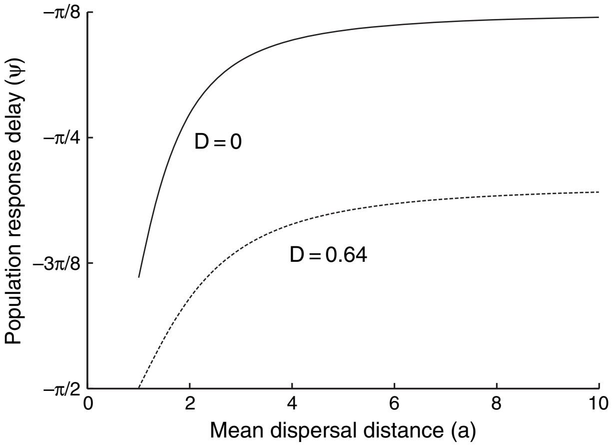

Figure 3 Population response delay ψ vs. mean dispersal distance. The population is perfectly out of phase with the environment when $\psi = -\pi$ and perfectly in phase with the environment (no delay) when $\psi = 0$. (See the expressions for ν_i and ψ in Appendix S1.) Increasing the mean dispersal distance reduces delay. (ψ gets closer to zero as a increases.) Dispersal does not reduce delay as much in the presence of dormancy. The population response delay depends on the precise spatial and temporal scale of environmental variation. (Recall that a random environment is composed of a mixture of variation at fast and slow speeds, small and large spatial extents.) This plot was created using sinusoidal variation with a spatial period of 12 and a temporal period of 16. Similar patterns are found at other spatial and temporal scales.

A brief word on branching points

An ESS need not exist. If the temporal correlation length is sufficiently short, genotypes with different mean dispersal lengths may coexist. Figure 4 shows how an initially monomorphic population is drawn to an equilibrium via a series of invasions. When the resident's mean dispersal distance is sufficiently close to the equilibrium value, the equilibrium reveals itself to be a branching point (Geritz *et al.* 1998) and the population becomes polymorphic, consisting of subpopulations with dispersal distances above and below the branching point value.

Branching points were termed evolutionary compatible strategies (ECS) by Cohen & Levin (1991), who defined them as strategies 'that can invade any other single type but also [are] open to invasion by any type'. Cohen and Levin found ECSs when there was underlying spatial

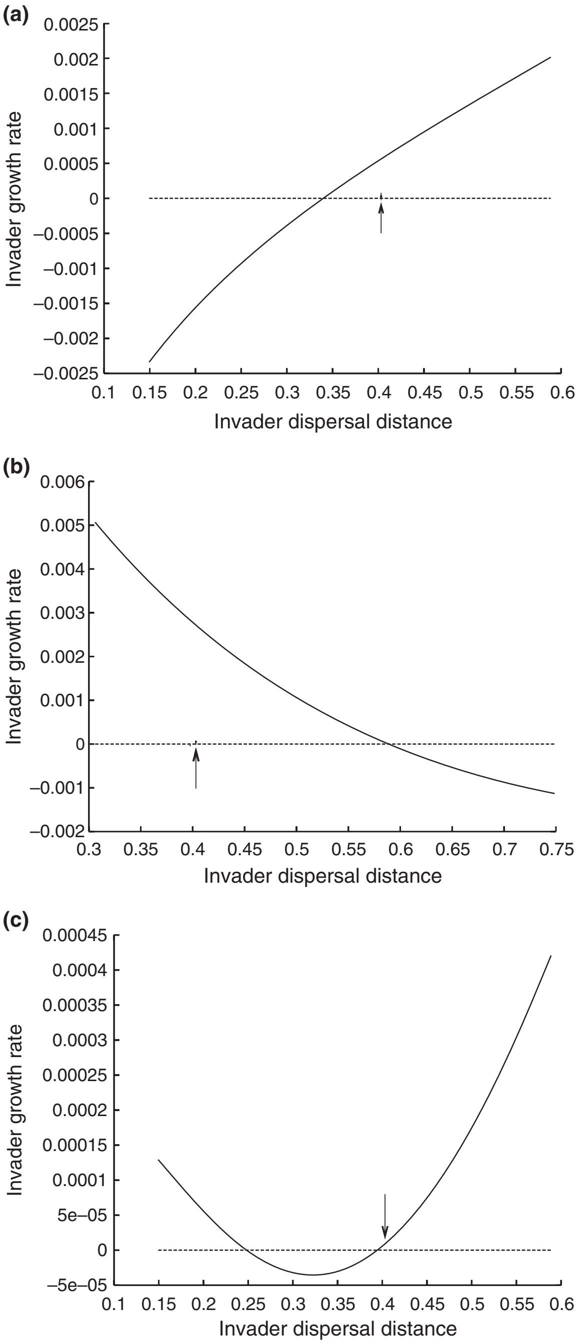

Figure 4 Invader long-run growth rate for mean resident dispersal distance above the branching point, below the branching point, and near the branching point. Here, $D = 0$, $\xi = 0$, $\tau = 1$, which means that the equilibrium point $a^* = 0.4031$, indicated by the arrows, is a branching point. In (a) $a_r < a^*$ ($a_r = 0.3399$). Invasion is possible for $a_i > a_r$ and so the resident dispersal distance moves towards a^*. In (b) $a_r > a^*$ ($a_r = 0.5888$). Invasion is possible for $a_i < a_r$ and the resident dispersal distance moves towards a^*. In (c) a_r is just below a^* ($a_r = 0.3945$). Invasion is possible both for $a_i > a_r$ and for a_i less than *c.* 0.25. Two subpopulations arise with different dispersal distances.

heterogeneity, so that some spots were more likely to experience favourable conditions than others, and when environmental conditions in successive years were negatively correlated. Others have found branching points when environmental conditions fluctuate temporally and habitat patches are of different sizes (McPeek & Holt 1992; Mathias *et al.* 2001). While the environment does vary at multiple spatial scales in the present study, so that one can think of there being favourable 'patches' of different sizes, the situation seems importantly different from those of earlier studies, for here the variation at different scales is superimposed. Instead of big and small habitat patches, here we have microhabitat variation superimposed on large-scale habitat variation.

The larger the spatial correlation length, the larger the temporal correlation length must be before the population switches from polymorphic to monomorphic (Fig. 1). It seems likely that when the temporal correlation length is small, far-dispersing morphs are successful because they avoid getting stuck in a habitat 'patch' that is becoming unfavourable. However, short-dispersing morphs also persist in the system because they are able to accumulate in favourable (if ephemeral) patches. Tracking spatial variation in environmental conditions in this way becomes more difficult as the spatial correlation length decreases – it is hard to retain offspring in a tiny habitat patch – and so polymorphisms become less likely as ξ decreases.

Dormancy increases the value of the branching point distance just as it increases the value of the ESS distance. Finding the actual dispersal distances and their relative frequencies is beyond the scope of this study. Nonetheless, it may be possible to get a hint of what happens by considering all-or-nothing dispersal, in which a fraction p of seeds disperse globally and the rest do not disperse. Using the same analysis on this simplified form of dispersal, we see that dormancy reduces the optimal fraction of dispersing seeds if temporal correlations are small enough (τ below *c.* 0.9 for $\xi = 0$), in agreement with the traditional dormancy–dispersal tradeoff (Fig. 5). For larger τ, dormancy increases the optimal fraction of dispersers. (However, dormancy seems to have little effect on the dispersal fraction unless spatial correlations are very small.) Figure 5 suggests that in an environment with sufficiently small but nonzero temporal correlations, dormancy may decrease the fraction of far-dispersing seeds in a polymorphic strategy.

DISCUSSION

In summary, dispersal has two effects on populations and these may prove costly or beneficial. First, dispersal distributes the population more evenly in space. This is a benefit in a rapidly changing environment, where without dispersal, populations would be concentrated in unfavour-

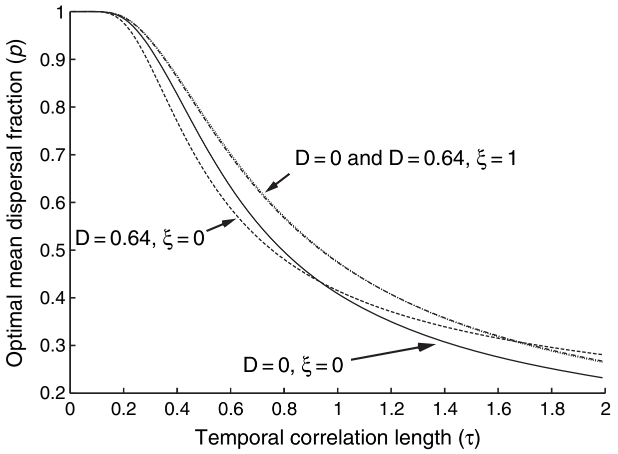

Figure 5 Optimal mean dispersal fraction (*p*) vs. the temporal correlation length (τ) for different dormancies (D) and different spatial correlation lengths (ξ). Here we assume all-or-nothing dispersal, in which a fraction p of the seeds disperse globally and the rest do not disperse. In the absence of spatial correlations ($\xi = 0$), increasing dormancy increases the optimal dispersal fraction for τ less than *c.* 0.9 and reduces the optimal dispersal fraction for larger temporal correlations. Dormancy has little effect on the optimal dispersal fraction in the presence of even modest spatial correlations.

able areas, and a cost in a slowly changing environment, where the population would be concentrated in favourable areas, were it not for dispersal. Second, dispersal reduces the delay between environmental change and the population's local response, which is always beneficial. The optimal dispersal distance is determined by balancing the costs and benefits. Dormancy changes the optimal dispersal distance by altering this balance, adding a net benefit so that for environments with positive temporal correlations, the ESS dispersal distance increases (Fig. 1). Far from reducing the need for dispersal, dormancy partially undoes the effect of dispersal, so that when dormancy is present, dispersal must be higher to compensate.

There need not be a single optimal dispersal distance. As the temporal correlation length is reduced, ESSs give way to branching points, and the population becomes polymorphic. The larger the spatial correlation length, the larger the temporal correlation length at which the population switches from being monomorphic to polymorphic (Fig. 1). Dispersal polymorphisms are known to exist for a number of species, especially those in the composite family. For example, in the composite family annual *Heterotheca latifolia* (now called *Heterotheca subaxillaris*), disc flowers produce a wind-dispersed pappus that enables long-distance dispersal, while ray flowers do not (Venable & Levin 1985). An examination of all-or-nothing dispersal, in which a fraction p of seeds disperse globally and the rest do not disperse, suggests that for sufficiently small temporal correlation lengths, dormancy may reduce the optimal fraction of long-range dispersers in a polymorphism, in line with the traditional dormancy–dispersal tradeoff (Fig. 5). There is some evidence of this happening in composite flowers with polymorphic achenes. For example, peripheral achenes of *Crepis sancta* have greater dormancy and less dispersal ability compared with central achenes (Imbert 1999). However, the peripheral achenes of *Bidens frondosa* have both less dormancy and less dispersal ability, in conflict with the traditional dormancy–dispersal tradeoff (Brandel 2004).

Empirical evidence on how dormancy affects dispersal is ambiguous. In agreement with the current findings, Gravuer *et al.* (2003) found that within populations of the asteraceous perennial *Liatris scariosa*, germination is somewhat negatively correlated with expected dispersal distance ($r = -0.376$). However, Rees (1993) found that species with less seed dormancy were significantly more likely to have seeds with 'burs, awns, spiny calyxes, wings, plumes, adhesive mucilage', or seeds dispersed via ingestion. How might we reconcile these findings with each other and with the current study?

First, in natural systems, the evolution of dispersal is entangled with that of other traits. For example, seeds with large mass usually disperse shorter distances (Jongejans & Schippers 1999), and seed mass has its own relationship with dormancy. Large seeds may allow plants to establish themselves in less favourable environments, reducing the need for dormancy (Pake & Venable 1996), although Rees (1996) found this to be true only for seeds with efficient mechanisms of dispersal. Gravuer *et al.* suggest that their results appear to be driven by a positive correlation between seed mass and germination success.

Second, the current study has only concerned itself with whether dormancy and dispersal can substitute for each other as risk reduction mechanisms and therefore has only considered the optimal dispersal distance for a given level of dormancy. If both traits were allowed to co-evolve, it is possible that a different relationship between dormancy and dispersal might emerge. Modelling the co-evolution of dormancy, dispersal, and seed size, Venable & Brown (1988) found that in an environment that is correlated in time but not in space, increased dormancy is associated with reduced dispersal. However, spatial correlations may matter. Of the two risk reduction mechanisms, only dispersal responds to spatial correlations. A longer spatial correlation length will result in selection for higher dispersal, which may then reduce selection for dormancy.

It is also important to remember that species do not evolve in isolation. Selective pressures depend on which other species are present in the community, and an inferior competitor may be able to invade a system if it has a dispersal distance which is well suited to its physical and competitive environment. For example, in a physical environment which is changing relatively rapidly, an inferior competitor may be able to persist by taking advantage of newly favourable habitat not yet found by the superior competitor (the 'competition–colonization tradeoff'; Tilman 1994). In a slowly changing environment, an inferior competitor may be able to persist if it can take advantage of gaps left when the superior competitor grows in a clustered fashion (Bolker & Pacala 1999; Murrell & Law 2003) or if, through short-range dispersal, it is better than the superior competitor at retaining its offspring in favourable locations (Snyder & Chesson 2003).

Finally, we should consider the character of natural environmental variation. The current study suggests that the traditional dormancy–dispersal tradeoff may hold if the temporal correlation length is small enough and if we consider the proportion of long-range dispersers in a polymorphism instead of mean dispersal distance. A meta-analysis by Vasseur & Yodzis (2004) suggests that many physical characteristics of terrestrial environments, such as precipitation, degree days, and winter severity index, are positively correlated in time but with small temporal correlation lengths. (Their variational spectra are close to 'white noise'.) It is not clear how the resulting environmental responses would be correlated – the current study concerns itself with correlations in an environmental response (here fecundity), not physical characteristics of the environment – but these results give an added incentive to understanding what happens for small temporal correlation lengths.

In summary, I have found that in an environment with a positive temporal autocorrelation, increasing dormancy increases the optimal mean dispersal distance or, if there is no unique optimum, increases the branching point. If the reverse is true in natural populations, then we cannot invoke the traditional explanation that dormancy and dispersal are equivalent forms of risk reduction and that the presence of one reduces the need for the other. The next steps seem clear. Empirically, we would like more data on whether dormancy is indeed associated with shorter dispersal distances. Theoretically, we need to understand what happens when dormancy and dispersal levels co-evolve, a study I have already begun. We also need to uncover the nature of the dispersal polymorphism predicted for small temporal correlation lengths: what dispersal distances are ultimately selected for and is it true that dormancy may increase or decrease the proportion of long-range dispersers, depending on the correlation length? Refining our ideas in this area will lead to a deeper understanding of one of the central issues of ecology: how organisms cope with unpredictability.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Derivation of the optimality condition.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1742-4658.2006.00962.x

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