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Leaving home ain't easy: non-local seed dispersal is only evolutionarily stable in highly unpredictable environments

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It is widely understood that in the presence of asynchronous environmental variation, seeds disperse to escape disturbances, avoid crowding or colonize newly favourable habitat before a superior competitor can arrive. If seeds are dispersing for any of these reasons, it seems intuitive that they should travel far enough to reach conditions uncorrelated with their natal environment: why 'escape in space' only to land somewhere more or less like where they started? However, in this paper, I present a series of mathematical experiments which show that the evolutionarily stable mean dispersal distance remains well short of the spatial correlation length of the environmental variation, regardless of disturbance severity, coevolution with a superior competitor or the presence of a small fraction of seeds which travel well beyond the mean distance. Non-local dispersal arises only as part of a polymorphism that evolves when favourable conditions are fleeting. To the degree that non-local dispersal is a response to environmental variation, it appears to be a response to environmental unpredictability.

Keywords: dispersal; environmental variation; evolutionarily stable state; achene dimorphism; bet hedging; competition–colonization tradeoff

1. INTRODUCTION

Seeds disperse in part because environmental conditions vary. Environmental variation causes seeds to disperse as a way of escaping disturbances (locally and temporarily unfavourable conditions) and as a way of escaping the crowding that occurs in more favourable areas [1–4]. Environmental variation can also encourage dispersal as part of a fugitive strategy, allowing inferior competitors to persist by being the first to exploit newly favourable areas [5–7].

But how far should seeds go? If seeds are dispersing to avoid crowding/competitors, escape disturbances or find newly favourable habitat, intuition suggests that they should travel far enough to find novel environments. Why disperse if you are only going to land somewhere much like where you started, affected by the same crowd of competitors, subject to the same disturbances? The distance over which environmental conditions (including disturbances) are more or less the same is called the spatial correlation length. Putting this intuition in more quantitative language then, we might expect that the mean dispersal distance will be approximately equal to or greater than the spatial correlation length of the environmental variation, so that a large fraction of the seeds land in environments uncorrelated with their natal environment. I will refer to this as non-local dispersal. Kin selection [8] and the risk of inbreeding depression [9,10] also select for increased dispersal, but in this paper, I wish to test intuition and consider the effect of environmental variation alone.

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I have found that while non-local dispersal can arise from environmental variation under some circumstances, non-local dispersal is not necessary to avoid disturbance in general, nor does it come about as a coexistence mechanism. In this paper, I find the evolutionarily stable (ES) mean dispersal distances for (i) species evolving in isolation in the presence of moderate, asynchronous variation in fecundity; (ii) an inferior and a superior competitor coevolving in the presence of moderate or severe variation in fecundity; and (iii) species evolving in isolation with a caricature of ballistic dispersal (all seeds travel the same distance). These investigations produce three main results.

First, the dispersal distances are not much different whether environmental variation is moderate or severe. This suggests that a population can escape localized disasters as long as favourable conditions last long enough that repeated dispersal events can spread the lineage beyond the danger zone by the time conditions become unfavourable.

Second, co-evolved dispersal distances are not very different from dispersal distances which have evolved in isolation. This suggests that while 'fugitive' species may disperse long distances, environmental variation and competitive imbalances alone are not enough to make this a viable strategy.

Third, dispersal distances are not much different whether a few seeds can travel well beyond the mean or all seeds travel the same distance. This suggests that the population is not being rescued by the small proportion of seeds which travel unusually far.

The only times I found non-local dispersal were as parts of dispersal polymorphisms, present when the environment was highly unpredictable (small temporal correlation length). In this case, favourable conditions

do not last multiple generations, and so a lineage cannot escape localized disturbances through a series of short hops. Instead, plants balance the benefits of local retention and bet hedging by keeping a portion of seeds close to home, in a currently favourable area, and sending the rest far away, in case local conditions are unfavourable next year. Note that a literal polymorphism is not necessary. Having multiple dispersal processes with different mean distances would accomplish the same end: for example, seeds may disperse a short distance by passive falling, then a portion of the seeds may be found and cached by rodents.

In the following section, I present my model. Section 3 presents the results of a series of mathematical experiments based on versions of that model. I conclude with a discussion, which includes suggestions on how these predictions might be tested. The details of the mathematics can be found in the electronic supplementary material, appendix S2.

2. MODEL

The number of annual seeds at location x at time t is $n_1(x, t)$ while the number of perennial adults is $n_2(x, t)$. Seeds germinate with probability g_j ($j=1,2$). Annual seeds which fail to germinate survive in the seedbank with probability s_1 , so that the proportion of dormant seeds is $s_1(1 - g_1)$. Perennial adults survive with probability s_2 .

Adult fecundity is $F_j(x, t)$, which varies stochastically with space and time because of variable environmental conditions. We can think of this variation as a form of disturbance. Fecundity is positively correlated in space and time, with spatial correlation length ξ and temporal correlation length τ .

$$\begin{aligned} \text{Cov}(F_j(x, t), F_k(x + x', t + t'))_{x,t} \\ = \cos(\theta) \langle F_j \rangle_{x,t} \langle F_k \rangle_{x,t} V \exp\left(\frac{-x'}{\xi}\right) \exp\left(-\frac{t'}{\tau}\right). \end{aligned} \quad (2.1)$$

That is, conditions are roughly similar out to a distance ξ for a time τ . Here, $\langle F_j \rangle_{x,t}$ is the spatiotemporal average of fecundity F_j and θ expresses the degree to which species j and k prefer the same habitat ($\theta=0$, prefer identical environmental conditions; $\theta=\pi$, prefer opposite conditions). V is the square of the coefficient of variation—the variance of F_j is $\langle F_j \rangle_{x,t}^2 V$ —and is the same for both species, so that both species experience similar proportional fluctuations in fecundity. We can thus tune the severity of disturbance (by adjusting V), the spatial scale of the disturbance (ξ), and the temporal scale of the disturbance (τ). Of course, in real environments, there may also be some permanent spatial heterogeneity in addition to disturbances. However, permanent heterogeneity will select for shorter dispersal distances. Wishing to be conservative and select for the longest possible distances, I use equation (2.1) and ignore permanent heterogeneity.

Seed production is reduced by competition from neighbouring annuals and perennials: an adult produces $F_j(x, t)/C_j(x, t)$ seeds, where $C_j(x, t)$ is the competition it experiences. Closer neighbours have a stronger competitive effect. This is accounted for by letting competition

depend on weighted averages of the local annual and perennial populations, where the weighting function $U_{jk}(z)$, called a competition kernel, weights closer competitors more heavily. For all calculations in this paper, $U_{jk}(z) = \exp(-|z|/b_{jk})/(2b_{jk})$, so that b_{jk} represents something like a competitive radius for the effect of species k on species j . Perennials are stronger competitors than annuals. The competitive effects of annuals and perennials are therefore multiplied by a factor γ_{jk} ($j, k=1,2$), denoting the strength of competitor k against competitor j . Thus,

$$\begin{aligned} C_j(x, t) = \gamma_{j1} \int_{-\infty}^{\infty} U_{j1}(x-y) g_1 n_1(y, t) dy \\ + \gamma_{j2} \int_{-\infty}^{\infty} U_{j2}(x-y) n_2(y, t) dy. \end{aligned} \quad (2.2)$$

(Note that the number of annual adults at (y, t) is $g_1 n_1(y, t)$, whereas the number of perennial adults is simply $n_2(y, t)$.)

Seeds disperse a distance z from their parent with probability $k_j(z)$. The dispersal kernel takes the form $k_j(z) = \exp(-|z|/a_j)/(2a_j)$, so that the mean dispersal distance is a_j and a few offspring travel much farther than the mean dispersal distance, while the majority travel less than the mean. It is the mean dispersal distance which we are allowing to evolve. This kernel form is what one would expect if seeds dropped out of the airstream at a constant probability per unit distance and is leptokurtic, as most real dispersal kernels are [11].

The full dynamics are thus

$$\begin{aligned} n_1(x, t + 1) = \int_{-\infty}^{\infty} k_1(x-y) \frac{g_1 F_1(y, t) n_1(y, t)}{C_1(y, t)} dy \\ + s_1(1 - g_1) n_1(x, t) \end{aligned} \quad (2.3)$$

and

$$\begin{aligned} n_2(x, t + 1) = g_2 \int_{-\infty}^{\infty} k_2(x-y) \frac{F_2(y, t) n_2(y, t)}{C_2(y, t)} dy \\ + s_2 n_2(x, t). \end{aligned} \quad (2.4)$$

In keeping with typical perennial and annual life-history strategies, I assume that the perennial is a better competitor but has lower fecundity. Drawing on data from California grasslands [12,13], I set annual fecundity (F_1) to be 200 and perennial fecundity (F_2) to be 45. I choose competition coefficients $\gamma_{11} = 0.6$, $\gamma_{21} = 0.2$ and $\gamma_{22} = \gamma_{12} = 1$. This choice is consistent with the finding that competition imposed on annuals by other annuals is less than competition imposed on annuals by adult perennials [12]. I choose perennial survival (s_2) to be 0.8, giving a mean lifetime of 20 years and let annual seed survival be 0.5 (mean lifetime 3 years). The annual germination rate (g_1) is 0.045 while the perennial germination rate (g_2) is 0.07. There is little data on the spatial scale of competition. The calculations for the figures were done using $b_{jk} = 1$ m for all species combinations, but I have redone many calculations for $b_{jk} = 0.1$ m and the results are qualitatively similar.

3. A SERIES OF MATHEMATICAL EXPERIMENTS

In order to explore the importance of various factors in driving the evolution of non-local dispersal, I consider several model variants.

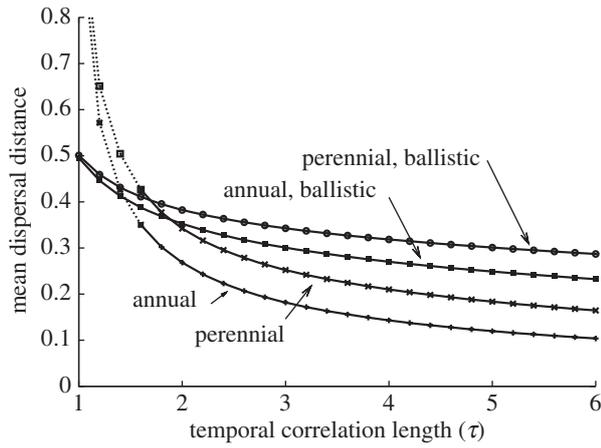


Figure 1. Evolutionarily stable mean dispersal distance evolved in isolation, $\xi = 1$ and $V = 0.1$ (moderate environmental variation). Solid lines represent evolutionarily stable states while dotted lines represent branching points. Results are shown for both exponential and ballistic dispersal.

(a) Monoculture evolution with moderate variation

In the baseline model, annuals and perennials evolve in isolation, subject to moderate variation in fecundity ($V = 0.1$, coefficient of variation = 0.32). Here an evolutionarily stable strategy (ESS) can be found largely analytically. The fitness of a would-be invader is given by its long-run growth rate in the presence of the resident and is a function of the dispersal distances of both invader and resident. This long-run growth rate can be approximately calculated by assuming that both the environmental variation and the population variation are small and writing a second-order approximation for long-run growth, as in Snyder [14]. The ESS is then found by maximizing the invader growth as a function of resident dispersal distance and determining when the optimal invader distance is equal to the resident distance: such a state is uninvasible by nearby strategies.

As can be seen in figure 1, dispersal distance increases for both the annual and the perennial as the environment becomes less predictable (τ decreases) but as long as there is an ESS, mean dispersal distance is always well short of the spatial correlation length: most seeds remain in an environment similar to their natal one. Note that for very unpredictable environments ($\tau < 1.5$ here), we get a dispersal polymorphism instead of an ESS. A number of studies have found dispersal polymorphisms in spatially heterogeneous environments [14–17]. We will return to polymorphisms in the final subsection.

(b) Coevolution with moderate variation

The next thought is that perhaps non-local dispersal would evolve as part of a fugitive strategy. A number of researchers have proposed that an inferior competitor might coexist with a superior competitor by being quicker to find and exploit newly favourable habitat [5–7]. Let us then consider the coevolution of the annual and perennial.

The analysis is similar in flavour to the baseline model, if more difficult in practice. Invader fitness is now the long-run growth rate of an invader in the presence of both an annual and a perennial resident, and we must consider both annual and perennial invaders. We

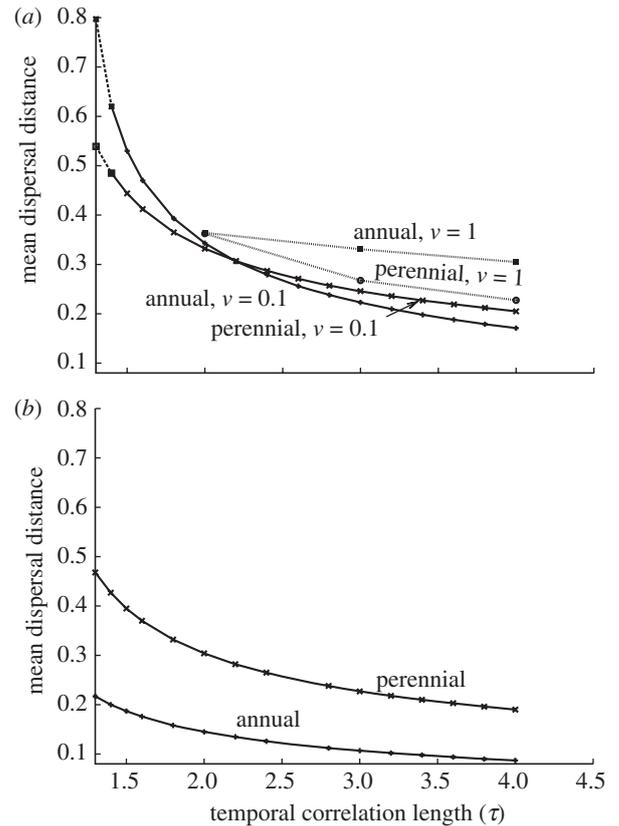


Figure 2. Co-evolved mean dispersal distances, $\xi = 1$. Solid lines represent evolutionarily stable states while dotted lines represent branching points. (a) Both species prefer the same conditions ($\theta = 0$). Results are shown for both moderate ($V = 0.1$) and severe ($V = 1$) environmental variation. (b) The species prefer opposite conditions ($\theta = \pi$).

maximize annual invader fitness as a function of annual and perennial resident distances and determine where the optimal annual invader distance is equal to the resident annual distance. This gives us the ES annual dispersal as a function of perennial dispersal. Reversing roles, we can find the ES perennial dispersal as a function of annual dispersal. The intersection of the two ES curves gives us our evolutionarily stable coalition (ESC). For this model, the curves never intersect in more than one point, so we need not worry about the effect of initial conditions. Full details can be found in the electronic supplementary material, appendix S2.

As with the baseline model, an ESC can be found with largely analytic methods if the environmental variation is moderate ($V = 0.1$). As with the baseline model, dispersal polymorphisms arise when the environment becomes sufficiently unpredictable. The actual dispersal distances depend on whether the two species prefer similar or different habitats, but as long as an ESC exists, the dispersal distances remain less than the spatial correlation length (figure 2).

(c) Severe disturbance

Perhaps the environmental variation is simply not severe enough? In the baseline and coevolutionary models, if seeds remain largely within a correlation length of their parent, then they will eventually experience an unfavourable environment, but even in the worst of times, they can

still reproduce. What if seed production were to fail completely?

The analytic methods used for the baseline and coevolutionary model are perturbative approaches that assume environmental variation and population variation are small. To explore extreme variation (coefficient of variation = 1), we must turn to simulations. The long-run growth rate (fitness) of an invader was determined by iterating the system equations (equation (2.3)) for 2048 time steps, recording the long-run growth rate, and averaging over 50 runs. Before each group of 50 runs, the system was simulated for 512 time steps with the residents only, to allow them to reach a stationary distribution. This stationary end state was then the starting point for each of the runs with the invader. Stochastic fecundity values were generated by using the square root of the power spectrum of the environmental autocovariance function (equation (2.1)) as the amplitude of a Fourier transform, adding a random phase and taking the inverse Fourier transform. This can produce negative values of fecundity. Negative values of $F_j(x,t)$ were set to zero, and values above $2\langle F_j \rangle_{x,t}$ were set to $2\langle F_j \rangle_{x,t}$ so as to preserve the mean value.

Results for coevolution in the presence of severe disturbance are shown in figure 2. We see that ES dispersal distances do increase, especially for the annual, but remain well below the spatial correlation length.

(d) *Ballistic dispersal*

The exponential dispersal kernel which we have used so far allows a small proportion of seeds to travel well beyond the mean dispersal distance, even though most seeds remain close to their parent. If even maximally disruptive disturbances do not select for non-local dispersal, perhaps these few far-travelling dispersers are enough to save the population? In this view, the bulk of an individual's offspring should remain close to home, since most offspring come from high fecundity areas that are likely to remain so for at least a little while (τ is positive). The tails of the dispersal kernel mean that there will always be a small fraction of seeds that travel far from home, and these are enough to allow the population to find newly favourable habitat.

We can test this idea by using an extreme caricature of ballistic dispersal: all seeds land precisely L metres to the right or left of their parent. ES dispersal distances are a little bit larger than for exponential dispersal, but not much (figure 1). Evidently, favourable periods last long enough that repeated dispersal events allow seeds to spread beyond their original natal area. Parents gain the benefit of local seed retention while conditions are good, but some offspring still make it beyond one spatial correlation length by the time conditions worsen.

(e) *Dispersal polymorphisms*

A number of studies have found that in the presence of spatial heterogeneity, dispersal polymorphisms are prone to develop [14–17]. In this study also, for both the baseline and coevolutionary models, dispersal polymorphisms exist for small temporal correlation lengths. When favourable periods do not last very long, it is not possible for seeds to be retained within their natal area yet still escape the correlated area by the time conditions

worsen. One response to a decreased temporal correlation length is to increase dispersal distance, giving up some of the benefits of local seed retention in favour of ensuring that some seeds escape a local disturbance. However, it appears that once the temporal correlation length gets small enough, populations adopt a different strategy, distributing some seeds locally and other seeds well beyond the local area.

I have looked for stable dispersal polymorphisms, following the same procedure used for the coevolution model but considering the coevolution of two dispersal morphs of the annual. I found no coexisting ESSs or further branching points, but simulating the system for $\xi=1$ and $\tau=1.4$ shows that the two morphs are pushed away from the original branching point. One morph quickly evolves to meander about a mean dispersal distance of 0.33 while the other morph evolves to disperse increasingly far, though neither species reaches a true ESS or branching point (figure in appendix S1). It may be that while we find no formal fitness maxima, the two morphs diverge until fitness becomes fairly flat, so that there is little selective pressure. Dispersal polymorphisms represent the only way I have found for non-local dispersal to evolve.

4. DISCUSSION

And so, can environmental variation alone select for non-local dispersal? The baseline model—a species evolving in isolation under the influence of moderate variation in space and time—says no. Any monomorphic ESS has a mean dispersal distance well below the spatial correlation length (figure 1). Increasing the severity of the variation increases dispersal distances somewhat, but not to the extent that they approach the spatial correlation length (figure 2). Neither do we get non-local dispersal by allowing an inferior competitor to co-evolve with a superior competitor: fugitive species are often characterized by excellent dispersal ability, but apparently this trait is driven by more than environmental variation (figure 2). One might think that perhaps the few seeds that travel well beyond the mean dispersal distance protect the lineage from local downturns in environmental conditions, allowing the mean dispersal distance to remain short. However, mean dispersal distance remains roughly the same even if we force all seeds to travel the same distance (figure 1). The only time we see non-local dispersal is when the environment is highly unpredictable (short temporal correlation length) and dispersal polymorphisms develop.

In determining ES seed dispersal distances, plants are trying to balance two goods. On the one hand, the most productive plants are in the most favourable areas, and so it makes sense to place offspring nearby, where conditions will also be favourable. On the other hand, local conditions will become unfavourable at some point, by which time some of the lineage needs to have spread into uncorrelated areas, lest the whole lineage experience decreased fitness. It appears that as long as favourable conditions do not fade too quickly, a parent can keep the benefits of locally placed offspring, because by the time conditions worsen, some of the lineage has spread beyond harm's way. However, as the environment becomes increasingly unpredictable, there comes a

point at which dispersal polymorphisms develop. Some offspring are retained locally, to take advantage of temporarily favourable conditions, while others are dispersed more widely as a form of bet hedging.

What evidence is there to test these ideas? Few papers have recorded the relevant scales of environmental variation when reporting on seed dispersal distances. Venable *et al.* [18] did not explicitly measure environmental variation but note that ‘...the bulk of seeds travel quite short distances relative to patterns of spatial heterogeneity operating on the scale of shrub/open habitat or greater.’ Platt & Weis [19] record dispersal distances for several fugitive species. Because these weak competitors are only able to establish on badger mounds, the typical distance between mounds is the relevant spatial scale of environmental variation. Mound frequency and moisture level both vary with topography, so by comparing the soil moisture level at which each species is most commonly found with intermound distances at that moisture level, we can get a rough comparison of mean dispersal distance and spatial scale. Perhaps unsurprisingly, mean dispersal distances were very roughly equal to the minimum intermound distances.

Ideally, one would record a plant’s eye view of environmental variation. If good measures of plant traits are available (fecundity, germination probability, whatever is thought to be the most important form of variation), then maximum likelihood methods can be used to estimate parameters for an exponentially decaying autocorrelation function, even if plants (and the associated measurements) are not regularly spaced [20]. Non-parametric estimates of autocovariance are also possible [21 and references therein]. If good measures of plant traits are not available, one might model plant traits (e.g. germination) as a function of physical variables such as moisture and temperature. A good spatiotemporal dataset would still be required, however.

The polymorphisms predicted by this study and others do exist: there are many plant species with dispersal polymorphisms, commonly in unpredictable environments [22]. In the Compositae family, for example, dispersal and germination properties often differ between central and peripheral achenes [23–25]. However, I believe a literal polymorphism is not necessary: a number of studies have found evidence for multiple dispersal processes, with different characteristic dispersal distances [26,27]. For example, Venable *et al.* [18] found that the seeds of desert annuals normally disperse short distances (mean dispersal distance less than 1 m) but that some seeds disperse widely (more than 10 m) via sheet wash after heavy rains.

Some of the conclusions of this paper echo the findings of other studies. The notion that an inferior competitor may persist by being a superior colonizer remains widely held, but several theoretical studies have chipped away at this idea [28,29]. In particular, Higgins & Cain [28] show that local dispersal reduces the need for an inferior competitor to be a superior colonizer, and that if the inferior competitor is not instantly displaced by the superior competitor, the need for superior colonization ability is eliminated. There have also been a number of spatially implicit patch models, in which a proportion of seeds remain in their natal patch while the others are distributed uniformly among the other patches. While there

can be no notion of dispersal distance in such a model, if conditions are uncorrelated between patches, then we can think of local dispersers as those which remain in their natal patch and non-local dispersers as those which leave. Cohen & Levin [1] finds that as the temporal correlation length increases, the proportion of seeds that disperse decreases, just as here, the mean dispersal distance decreases. Mathias *et al.* [15], Parvinen [16] and McPeck & Holt [30] have all found polymorphisms in the proportion of seeds that disperse when patch quality varies in space and time (without spatial or temporal correlations). It is reassuring to find the same phenomenon in this study.

The value of the current study is that it allows us to consider dispersal in a more natural way, using explicit dispersal distance instead of all-or-nothing dispersal. In addition to facilitating comparisons with empirical studies, this more nuanced approach allows us to see that in the absence of dispersal polymorphisms, the majority of seeds disperse locally. This is not apparent from the patch models. For example, Cohen & Levin [1] find that when next year is 50 per cent likely to be like this year, all seeds should leave the natal patch. (Dispersal is entirely non-local.) This geometrically decaying autocorrelation function is roughly equivalent to a temporal correlation length of 1.5 in the current study. For such a temporal correlation, I find a maximum mean dispersal distance of 0.6, corresponding to roughly 20 per cent non-local dispersal (20% of seeds travel beyond one spatial correlation length). Additionally, the current approach shows that dispersal polymorphisms are only present when the temporal correlation length is short, again emphasizing the special conditions required to evolve substantial non-local dispersal.

There may be ways besides polymorphisms that environmental variation can select for non-local dispersal. None of the model variants in this paper account for the discrete nature of individuals. Rather, the finite survival probabilities and the infinite tails of the dispersal kernel normally ensure that there is always at least a very small population everywhere. This may not be important: very small populations contribute very little to fitness. On the other hand, it may be that if local extinction is possible, then larger dispersal distances are necessary to recolonize empty areas.

It may also be possible to obtain non-local dispersal if two coevolving species do not perceive the environment as equally variable. Kisdi [31] presents a two-patch model in which species can evolve higher fitness on one patch or the other (specialist) or retain intermediate fitness in both (generalist). The dispersal rate is also allowed to evolve. If, in addition to intrinsic fitness differences between the two patches, habitat quality fluctuates, then a common outcome is the coexistence of a low-dispersing specialist with a high-dispersing generalist. That is, the species that experiences less fitness variation has a higher propensity to disperse. While this does not translate directly into longer dispersal distances, the results are suggestive.

Not all environmental variation can be described by the correlation function I have used in this paper. Many sites will have permanent spatial heterogeneity in addition to spatiotemporal variation, but permanent heterogeneity should reduce the ES dispersal distance, not increase it. Intuitively, if some sites are permanently better than others, seeds should be retained there. It is also true

that the environmental autocorrelation function may not drop off exponentially. This is especially true if plants are only likely to establish on small islands in a hostile matrix, e.g. serpentine soil endemics or the fugitive species in Platt & Weis's study, which were largely restricted to badger mounds. The concept of hospitable islands in a hostile sea is not that different from the model with severe environmental variation, however, in which fecundity was typically zero in bad places/times. It is not clear that changes in the shape of the correlation function should change the results substantially.

In conclusion, it is surprisingly difficult to get environmental variation to select for non-local variation, despite the common intuition that seeds disperse to find newly favourable habitat, avoid disturbances, or avoid competition in favourable areas. To the degree that non-local dispersal is a response to environmental variation, it appears to be a response to environmental unpredictability more than to disturbance severity or to the presence of a superior competitor.

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