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The evolution of non-random movement along clines

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ABSTRACT

Questions: Simple models of dispersal assume that it incurs evolutionary costs by inhibiting local adaptation. Is this still true when recognizing that individuals' decisions over whether and where to disperse are often a response to the environmental conditions they face? What are the implications of such conditional and directional dispersal behaviours for the evolution of dispersal itself?

Mathematical methods: Population genetic model of gene frequency change at two loci in a cline (spatial selection gradient) when dispersal rates depend on local fitness.

Key assumptions: The landscape is a linear array of equal-sized patches bounded by core populations. One locus is under direct selection and there is a gradient in juvenile survivorship with different genotypes being favoured on either side of an environmental transition zone. I compare models in which evolutionary changes in the cline spread out to affect dynamics in core populations with models where core populations are insulated from changes that occur within the cline. Population regulation applies after dispersal when there are limited opportunities to reproduce. The second locus governs the evolution of dispersiveness. Dispersing individuals bias their movements to climb local gradients in juvenile survivorship or expected fitness (juvenile survivorship and overcrowding).

Predictions: (1) When dispersal is directional and conditional, it does not impede local adaptation as much as when it is unresponsive to environmental conditions. It may even advance local adaptation. But more responsive dispersal can lead to overcrowding. Initially, the effect of dispersal on crowding dominates, but eventually the effect of dispersal on local adaptation becomes more important. (2) Dispersers abandon the cline centre when dispersal responds to juvenile survivorship, but cluster there when it responds to expected fitness. (3) When core populations are affected by changes in the cline, sigmoidal (as opposed to stepped) clines are maintained more effectively by dispersal that is responsive to the environment than by random dispersal.

Keywords: cline, conditional dispersal, directional dispersal, evolution of dispersal, fitness-dependent dispersal, gene flow, hybrid zone, indirect selection, local adaptation.

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INTRODUCTION

Dispersal is a complex response of phenotypes to their environment in many species, one that is often conditional and directional (Ims and Hjermann, 2001; Bowler and Benton, 2005). However, current understanding of the ecological and evolutionary consequences of dispersal is based on models that assume individuals' decisions over whether and where to disperse are fixed and unresponsive to environmental conditions (Lenormand, 2002; Hanski and Gaggiotti, 2004).

Basic predictions about dispersal change when models incorporate a richer representation of dispersal behaviours (Armsworth and Roughgarden, 2005a, 2005b). For example, cline models that assume fixed and unresponsive movement predict dispersal will smooth across environmental gradients when considering population differentiation within species (Lenormand, 2002). Moreover, these models predict dispersal will incur an indirect cost, because it impedes local adaptation (Balkau and Feldman, 1973; Billiard and Lenormand, 2005). However, patterns and processes in clines change when dispersal is a conditional and directional response by individuals to their environment (Armsworth and Roughgarden, 2008). The knock-on implications of more complicated dispersal behaviours for the indirect cost of dispersal inhibiting local adaptation in clines are unknown.

Clines are spatial gradients in genotypic and phenotypic characters within species. They are commonly associated with environmental transitions, such as gradients in soil types (Ross and Harrison, 2002). Acting in isolation in such a transition, selection would produce stepped changes in qualitative traits. However, unresponsive dispersal is assumed to carry individuals across the environmental transition to produce sigmoidal patterns in gene frequencies (Haldane, 1948; Slatkin, 1973; Lenormand, 2002). In this classic picture of clines, dispersal incurs an indirect cost, because individuals disperse away from habitats to which they were well-adapted into habitats where they are less well-suited (Balkau and Feldman, 1973; Kirkpatrick and Ravigne, 2002; Billiard and Lenormand, 2005).

The unresponsive dispersal assumptions that underpin classic cline models are challenged by recent studies on animal movement. For example, a mark–recapture study conducted inside one of the best studied clines, the transition between the fire-bellied toads *Bombina bombina* and *B. variegata* in Eastern and Central Europe, found that individual movement patterns within the centre of the cline were habitat and genotype dependent (MacCallum *et al.*, 1998). Individuals biased their movement away from habitats to which they were poorly suited and towards those where they were well-adapted. This movement pattern reflects similar findings in a range of very different taxa, including birds (Garant *et al.*, 2005), butterflies (Thomas and Singer, 1987), and snails (Erlandsson *et al.*, 1998; Cruz *et al.*, 2004).

Motivated by these and other empirical examples, Armsworth and Roughgarden (2008) re-examined the structure of clines under different assumptions about how animals move. We found that clines become steeper the more responsive dispersal is to the environment when individuals bias their dispersal to climb spatial gradients in fitness (*directed movement*). However, the particular details regarding dispersal behaviour determine whether this process eventually leads to a sigmoidal or stepped change in gene frequencies. Specifically, a smooth cline can be maintained even for perfectly responsive dispersal if dispersal responds to some components of fitness only (juvenile survivorship). However, the smooth cline is maintained by a different mechanism (biased dispersal out of the transition zone) to that maintaining smooth clines in classic models (diffusive dispersal across the transition zone). In contrast, clines eventually become stepped as the responsiveness of dispersal to the environment increases when dispersers respond to expected fitness (juvenile survivorship and overcrowding).

Here, I examine the consequences of directed movement for the second prediction of classic cline models, namely the indirect fitness cost associated with dispersal impeding local adaptation. One might expect that this cost would simply be lessened when treating dispersal as a response to environmental conditions, a prediction supported by two-patch models (Armsworth and Roughgarden, 2005b). In fact, the spatially extended cline models I present offer a much richer vein of results, including, for example, the prediction that dispersal costs associated with directed movement may often be larger than those predicted for unresponsive, diffusive movements.

There are important theoretical precursors to this study. Some authors have examined other consequences of fitness-dependent movement (Grindrod, 1988; Ruxton and Rohani, 1998; Hadany *et al.*, 2004; Armsworth and Roughgarden, 2005a, 2005b; Abrams, 2007; Abrams *et al.*, 2007; Amarasekare, 2007). These studies build on earlier works on habitat selection (reviewed in Rosenzweig, 1991). There are classic cline models that assume diffusive dispersal (Haldane, 1948; Slatkin, 1973; Lenormand, 2002). Of these, only Nagylaki and Moody (1980) consider genotype-dependent movement and they restrict attention to situations where there is no selection. Finally, there are studies on the evolution of dispersal. Many authors have examined the evolution of conditional dispersal when environmental conditions affect populations in a uniform manner (e.g. McPeek and Holt, 1992; Poethke and Hovestadt, 2002). However, this precludes study of local adaptation. More pertinent are studies that examine how dispersal evolution responds to the indirect selection pressure generated in clines because dispersal inhibits local adaptation (Balkau and Feldman, 1973; Armsworth and Roughgarden, 2005a; Billiard and Lenormand, 2005). But these studies all consider two-patch environments and/or unresponsive movement.

METHODS

I use stepping stone models of a 50-patch linear landscape. I consider a diploid two-locus model in which generations are non-overlapping and individuals are hermaphroditic. I assume subpopulations are large enough that I can neglect drift. I also neglect mutation. I census at the gametic stage. Viability selection occurs during the juvenile stage. Individuals then disperse between neighbouring patches, and I do not include direct costs of dispersal (e.g. from increased mortality among dispersing individuals). Mating occurs within subpopulations after dispersal. I assume local resource constraints mean only a fixed number of individuals mate successfully in each patch and patch sizes are equal. I assume random union of gametes and that fecundity is constant. While stringent, these assumptions allow important simplifications and are not unusual for population genetics.

To examine local adaptation in clines, I assume one locus (the A locus) operates under direct selection. I examine a gradual fitness transition (Fig. 1A),

$$w_{i_{AA}} = \begin{cases} 1+s & \text{for } i \in [1 \ldots (L-T)/2] \\ 1+s\left(1-\frac{2i-(L-T+1)}{T}\right) & \text{for } i \in [(L-T)/2+1 \ldots (L+T)/2] \\ 1-s & \text{for } i \in [(L+T)/2+1 \ldots L] \end{cases} \qquad (1)$$

$$w_{i_{aa}} = 2 - w_{i_{AA}}$$

$$w_{i_{Aa}} = w_{i_{AA}}(1+d_A)/2 + w_{i_{aa}}(1-d_A)/2$$

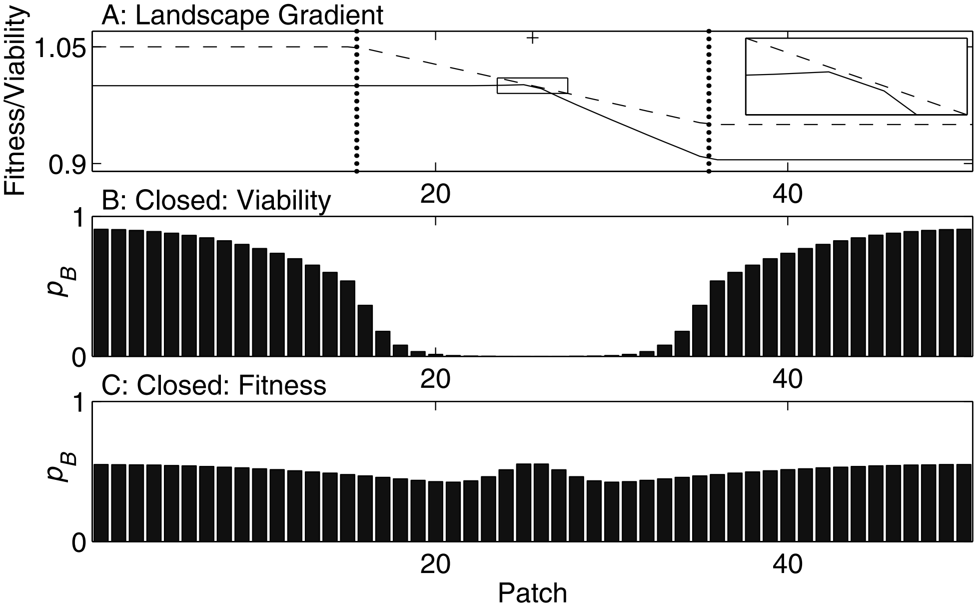

Fig. 1. *Landscape gradients and spatial distribution of dispersiveness for directed movement in closed landscapes.* (A) Dashed line in main panel shows the gradient in viability selection for an AA homozygote, w_{AA}. Juvenile survivorship declines linearly across the transition zone (bordered by dotted lines). Solid line in main panel shows the gradient in expected fitness ($w_{AA}/\overline{w}$) of an AA homozygote that is achieved before the introduction of the non-dispersive allele. For clarity, the inset (small rectangular panel) zooms in to show these curves at the centre of the transition zone in more detail. The inset highlights how the expected fitness increases slightly as the centre of the transition zone (marked with cross) is approached, because of competition to reproduce. (B, C) Spatial distribution of dispersive B alleles in closed landscapes when the mean frequency of dispersive alleles in the population $\overline{p_B} = 0.5$ for directed movement (B) in response to viability selection and (C) in response to expected fitness. Parameters: $[v, \sigma, s, d_A, d_B, r, L, T] = [0.6, 0.3, 0.05, 0, 0, 0.1, 50, 20]$.

Here, L and T are the sizes of the landscape and environmental transition and s determines the strength of selection. Each allele is at an advantage at one end of the landscape. Parameter $d_A \in [0, 1]$ determines dominance by A. Linear selection gradients have featured prominently in past cline models (e.g. Fisher, 1950; May *et al.*, 1975; Armsworth and Roughgarden, 2008). The results that I present are not sensitive to replacing this functional form with a smooth gradient of similar steepness.

I examine directed movement, in which individuals gather information on the quality of surrounding patches and bias their dispersal to climb spatial gradients in fitness. I examine a case where dispersal responds to one component of fitness (viability selection only) as well as dispersal that is fully fitness dependent (viability selection and crowding). Specifically, for directed movement that responds to viability selection only, the probability an $AABB$ individual moves from patch i to $i - 1$ is

$$\sigma_{(i-1)i_{AABB}} = \frac{\sigma_{BB}}{2}\left(\frac{v}{c}\left(\max(w_{i-1_{AA}} - w_{i_{AA}}, 0)\right) + (1 - v)\right), \tag{2}$$

and similarly for movements from i to $i + 1$. The probability that the individual does not disperse is $\sigma_{ii_{AABB}} = 1 - \sigma_{(i-1)i_{AABB}} - \sigma_{(i+1)i_{AABB}}$.

When considering conditional dispersal, one needs to distinguish between whether an organism is able to disperse should environmental conditions favour it and the actual movement patterns that are realized, because actual movement patterns combine the effects of the animal's ability to disperse with prevailing environmental conditions. Here, I focus on the evolution of physiological traits (for example, winged morphs in some insects) that make dispersal possible. I use the term 'dispersiveness' to describe the ability and likelihood that an individual will move when presented with a particular set of environmental cues. In equation (2), parameter σ_{BB} measures dispersiveness and governs the tendency of a BB homozygote to move.

Dispersal comprises both responsive and unresponsive movement components with parameter v determining their relative importance. Dispersal is entirely dependent on environmental stimuli when $v = 1$, whereas a fixed proportion of individuals disperse regardless of environmental conditions when $v = 0$. Juveniles gather information on the quality of surrounding habitats and the incentive to disperse is proportional to differences in survivorship between neighbouring patches.

The incentive to disperse in equation (2) does not reflect the density regulation that will apply before reproduction. I also examine directed movement when dispersal responds to fitness itself. In this version, I assume dispersal responds to cues about viability selection and local density experienced during the juvenile stage. Individuals then disperse in response to their expected fitness, giving

$$\sigma_{(i-1)i_{AA}} = \frac{\sigma}{2}\left(\frac{v}{c}\left(\max\left(\frac{w_{i-1_{AA}}}{\overline{w_{i-1}}} - \frac{w_{i_{AA}}}{\overline{w_i}}, 0\right)\right) + (1 - v)\right), \tag{3}$$

where

$$\overline{w_i} = w_{i_{AA}} p_i^2 + 2 w_{i_{Aa}} p_i q_i + w_{i_{aa}} q_i^2. \tag{4}$$

Because $\overline{w_i}$ depends on p, dispersal rates in equation (3) are not constant during evolution.

Scaling parameter c ensures the responsive and unresponsive movement components are of comparable magnitude

$$c = \begin{cases} 2s/T & \text{when dispersal responds to viablity only} \\ 4s/T & \text{when dispersal responds to expected fitness.} \end{cases} \tag{5}$$

To examine the evolution of dispersiveness, I assume that the second locus, the B locus, contains a neutral modifier governing this parameter. Specifically,

$$\sigma_{BB} = \sigma \qquad \sigma_{Bb} = \sigma(1 + d_B)/2 \qquad \sigma_{bb} = 0, \tag{6}$$

where σ governs the overall amount of movement going on and $d_B \in [-1, 1]$ describes dominance at the B locus. By combining equation (6) with relevant versions of equations (2) and (3), I obtained movement probabilities between adjacent habitat patches for each genotype.

I let x_{i_k} for $k = 1$–4 represent the frequencies of AB, Ab, aB, and ab gametes at mating in patch i. Taking Ab gametes as an example, the overall dynamics for gamete frequencies become

$$x_{i_2}(t+1) = \frac{\sum_{j=i-1}^{i+1} [\sigma_{ij} w_j]_2 x_{j_2}(t) + r\sigma_{ij_{AaBb}} w_{j_{Aa}} D_j}{\sum_{j=i-1}^{i+1} \sum_{k=1}^{4} [\sigma_{ij} w_j]_k x_{j_k}(t)}, \tag{7}$$

where $D_j = x_{j_1}x_{j_4} - x_{j_2}x_{j_3}$ is the linkage disequilibrium coefficient for patch j and r is the rate of recombination. Terms in square brackets are dispersal-weighted marginal fitnesses; for example,

$$[\sigma_{ij} w_j]_2 = \sigma_{ij_{AABb}} w_{j_{AA}} x_{j_1} + \sigma_{ij_{AAbb}} w_{j_{AA}} x_{j_2} + \sigma_{ij_{AaBb}} w_{j_{Aa}} x_{j_3} + \sigma_{ij_{Aabb}} w_{j_{Aa}} x_{j_4}. \tag{8}$$

Dynamics for the other gamete types are similar. I use p_A and p_B as a shorthand to describe the overall frequency of *A* and *B* alleles.

I compare two different assumptions about the landscape edges. First, I assume the landscape is a closed system and make the landscape boundaries reflecting. With this assumption, evolutionary changes in the hybrid zone have the potential to spread out into the core populations towards the landscape edges. With the second assumption, I treat the cline as an open system that is heavily influenced by dynamics within core populations but unable to influence dynamics there in turn. With this second, open landscape formulation, I assume the end patches remain fixed for the locally well-adapted, dispersive type (*AB* in patch 1 and *aB* in patch 50) regardless of what happens in the transition zone. Debates over whether the spread of evolutionary innovations that arise in hybrid zones is constrained by dynamics in adjoining core populations have persisted since at least Dobzhansky's writings on the topic nearly 70 years ago (Dobzhansky, 1940). With these two assumptions, I compare the two possibilities. My use of the terms 'open' and 'closed' here to describe evolutionary dynamics that are subject to outside influences or that are wholly self-contained is consistent with the use of these terms in other disciplines [including ecological models of population dynamics (Caley *et al.*, 1996; Murdoch *et al.*, 2006) and economic and demographic models (O'Sullivan, 2003)]. I review the relationship of these assumptions to other model formulations in population genetics later on.

Numerical solutions of the model are generated by forward iterating equation (7) along with its counterparts for the other gamete types. To seed the model, the dynamics are forward iterated for 5000 generations when only *AB* and *aB* types are present. This allows the dynamics to equilibrate to a stable cline at the *A* locus, which is determined by the interaction of dispersal and local adaptation. Then, I assume mutation gives rise to an *Ab* gamete in the centre of the transition zone and track evolution at both loci for a further 500,000 generations.

RESULTS

Unresponsive movement

The results for the case where $v = 0$ and dispersal is unresponsive to the environment are in line with theoretical expectations (Balkau and Feldman, 1973; May *et al.*, 1975; Kirkpatrick and Ravigne, 2002). Before the introduction of the non-dispersive allele, the gene frequency dynamics at the *A* locus equilibrate to a smooth cline in both the closed and open landscapes. If there were no dispersal at all, each A allele would head to fixation on the side of the transition zone where it was at a local advantage. But unresponsive dispersal smooths the stepped cline that would otherwise result by carrying individuals across the transition zone.

Closed landscape

In a closed, self-contained landscape, the smooth cline at the A locus persists for a long time after the introduction of the less dispersive b allele. But eventually, the non-dispersive b allele invades and heads towards fixation; dispersiveness is lost in the transition zone; and the cline becomes stepped, leaving two pure types isolated from one another (dotted curves in Figs. 2A and 3A). During its evolution, spatial gradients in dispersiveness are minimal, reflecting the tendency of unresponsive movement to homogenize populations.

Open landscape

In contrast, strong selection pressures maintain dispersal in core populations in the open landscape. This results in a sustained influx of dispersive individuals at the landscape edges and means dispersiveness cannot be lost altogether. The indirect selection pressure that drives dispersal evolution for the closed landscape is a relatively weak force, precisely because it is indirect, and cannot counteract the very strong selection I have assumed in the core populations. As such, the dispersal modifier does not invade in the open landscapes and the smooth cline at the A locus is maintained (trajectories marked with dots in Figs. 2C and 3C).

Movement responds to viability selection

When dispersal responds to viability selection, individuals react to the environmental gradient in the transition zone by biasing their movement towards the end of the landscape where they enjoy higher juvenile survivorship. Inside the transition zone (vertical dotted lines in Fig. 1A), an AA individual will bias its movement to the left to climb the survivorship gradient (dashed line in Fig. 1A). However, an AA individual outside the transition zone will express no directional preference because surrounding habitats are uniformly suitable or unsuitable. This movement pattern results in a steeper cline at the A locus for both the closed and open landscapes before the introduction of the non-dispersive allele, with the steepness depending on just how responsive dispersal is to the environment. However, gradual sigmoidal clines at the A locus are maintained even as v tends towards 1 and dispersal becomes fully responsive to the environment (Armsworth and Roughgarden, 2008).

Closed landscape

After its introduction, the non-dispersive allele spreads rapidly in the closed landscape when dispersal responds to viability selection, unlike the case where dispersal is unresponsive to the environment (Fig. 2A). Dispersive alleles are lost first from the heart of the transition zone, but retained for longer out towards the landscape peripheries (Fig. 1B). Because dispersal is lost quickly from the transition zone itself, the cline at the A locus can very quickly become stepped, a process that happens faster the more responsive dispersal is to the environment (Fig. 3A).

These dynamics are reversed over the long term. Eventually, the relative rate of loss of dispersiveness across the different dispersal behaviours reverses and more responsive dispersal behaviours allow some dispersiveness to be retained over the very long run

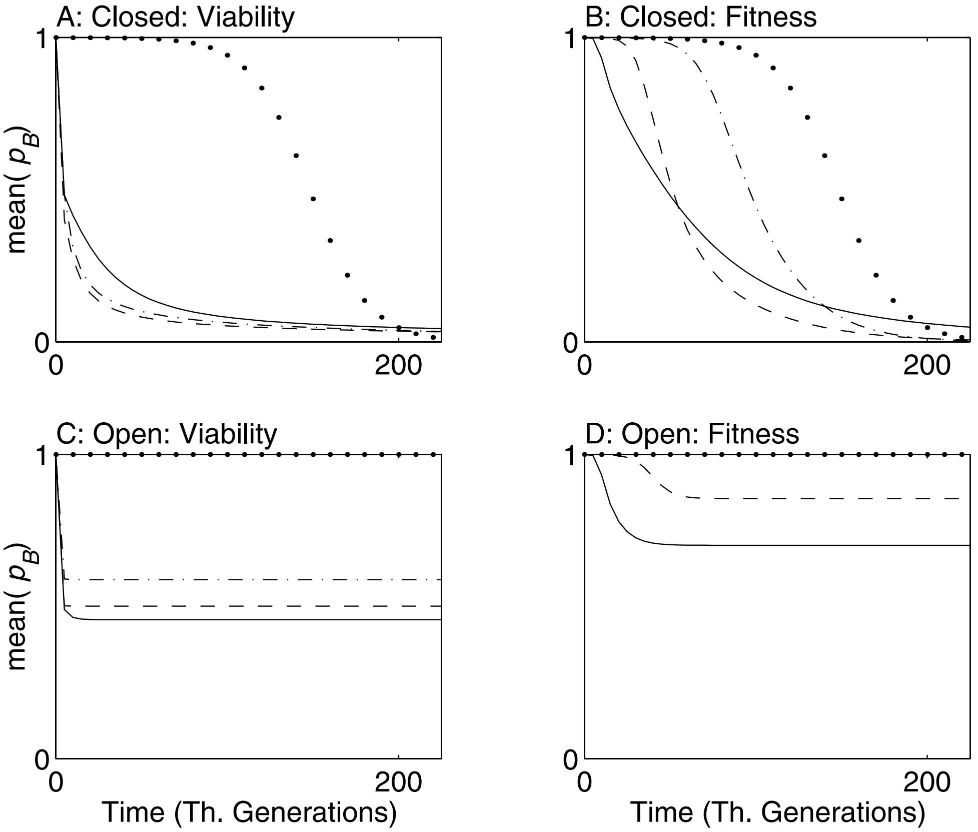

Fig. 2. *Evolution of dispersiveness*. Evolution of dispersiveness or, equivalently, change in the frequency of the B allele through time, (AC) when dispersal responds to viability selection and (BD) when it responds to expected fitness (AB) in closed landscapes and (CD) in open landscapes. Mean frequency of dispersive B alleles for differing levels of responsiveness of dispersal to environmental stimuli; dotted, dot-dash, dashed, and solid curves correspond to $v = [0, 0.3, 0.6, 0.9]$. Other parameters: $[\sigma, s, d_A, d_B, r, L, T] = [0.3, 0.05, 0, 0, 0.1, 50, 20]$.

more effectively than does entirely unresponsive dispersal (right-hand side in Fig. 2A). If dispersal contains a significant unresponsive component, this can allow smooth clines to persist for longer (comparing dotted and dot-dash trajectories in Fig. 3A).

To understand what is driving these dynamics, one needs to examine the indirect fitness consequences of dispersiveness associated with the different dispersal behaviours. This is complicated by the fact that the fitness consequences of dispersiveness vary in both space and time. I use a numerical experiment to illustrate the interplay of these forces shown in Fig. 4. To measure the fitness consequences of dispersal, I compared the number of copies of itself that an A allele successfully propagates through to the pre-dispersal stage in the next generation when it is combined into an AB gamete with the number of copies left when it is combined into an Ab gamete. I expressed this as a ratio of number of copies left by an Ab gamete divided by number of copies left by an AB gamete. If the ratio is greater than 1, there is an indirect fitness cost associated with dispersiveness and the non-dispersive allele

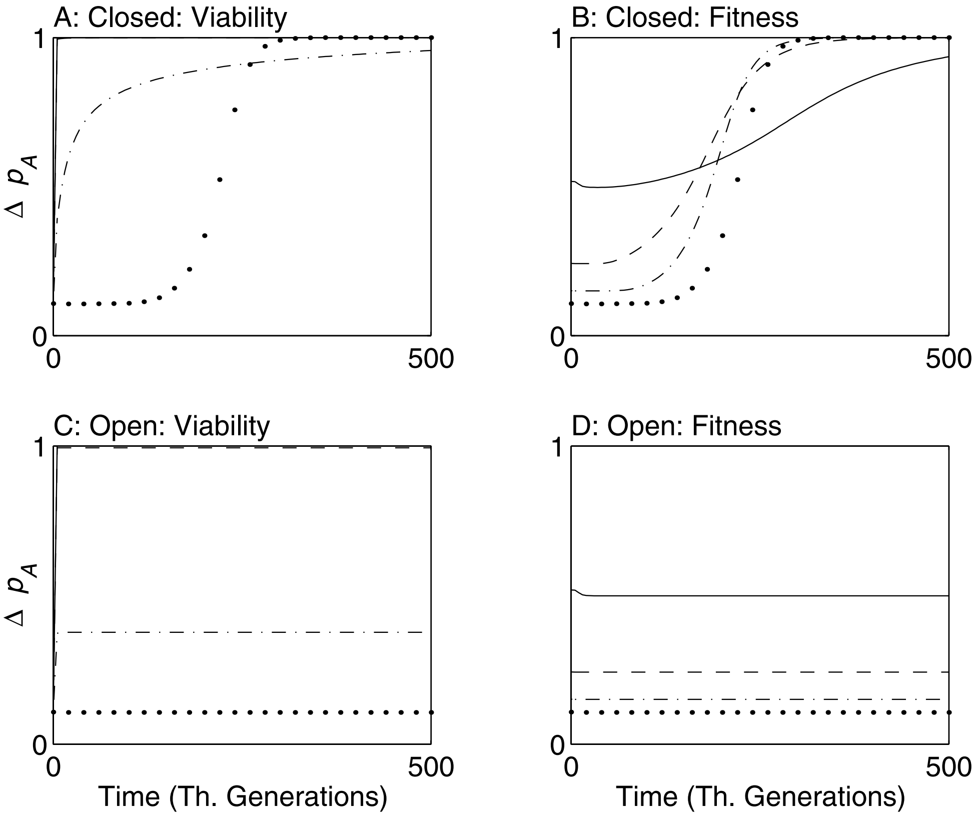

Fig. 3. *Steepness of cline at the A-locus during dispersal evolution.* The steepness of the cline in A-frequency measured as the difference between the frequency of A alleles in the two patches at the centre of the transition zone, Δp_A, as dispersiveness evolves (AC) when dispersal responds to viability selection and (BD) when it responds to expected fitness (AB) in closed landscapes and (CD) in open landscapes. Steepness shown for differing levels of responsiveness of dispersal to the environment: $v = [0, 0.3, 0.6, 0.9]$ for dotted, dot-dash, dashed, and solid curves respectively. Other parameters: $[\sigma, s, d_A, d_B, r, L, T] = [0.3, 0.05, 0, 0, 0.1, 50, 20]$.

has an advantage. An explicit statement of the relevant ratios is given in the Appendix. To simplify dynamics, I illustrate for the case where the recombination rate is zero and, for this illustration alone, I introduced the b allele into both an Ab and ab gamete initially to allow it to spread across the genetic background, despite having $r = 0$.

Once again, the interplay between viability selection and overcrowding determines the fitness costs involved. To separate the effects of these two forces, I compared the number of copies that the A allele would contribute when both viability selection and population regulation were acting (the relevant ratio is shown as a solid line in Fig. 4A, C), when only viability selection was acting (dotted line in Fig. 4A, C), and when only population regulation was acting (dashed line in Fig. 4A, C). Because the relative importance of the two forces changes through time, I illustrate the importance of these fitness costs in the early stages of the evolution of dispersiveness (when the mean frequency of the B allele equals 0.9) and later stages (when mean(p_B) = 0.1).

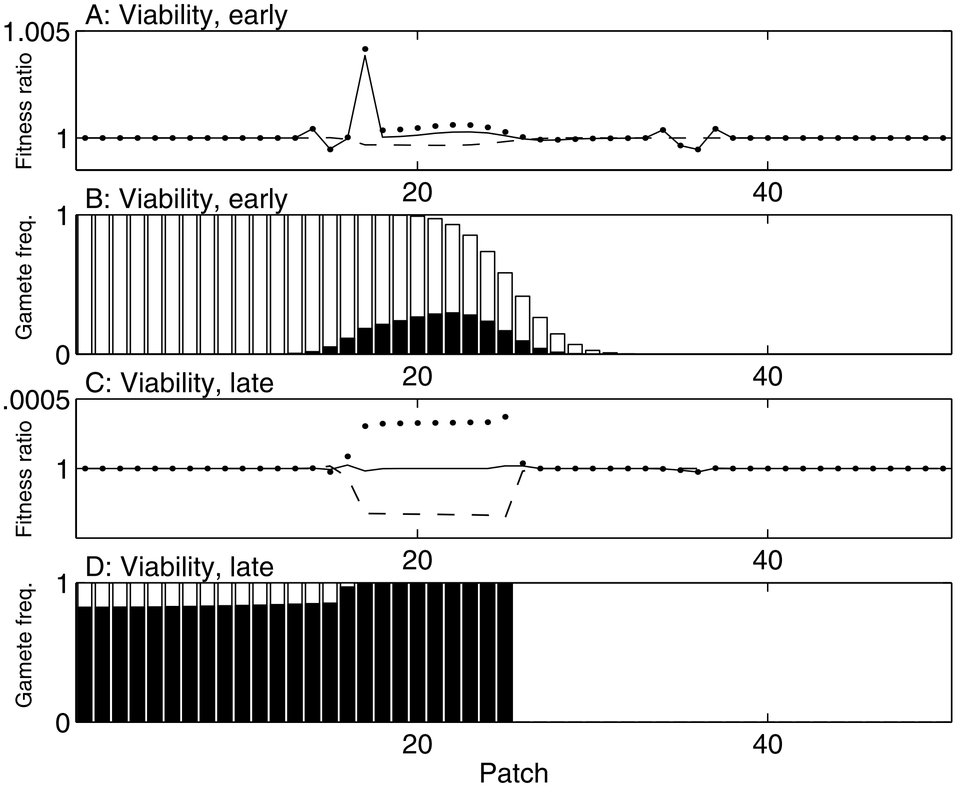

Fig. 4. *Indirect costs of dispersiveness.* To compute the indirect costs of dispersiveness, I calculated the number of copies of an *A* allele successfully propagated into the next generation by a non-dispersive *Ab* gamete and a dispersive *AB* gamete. The solid curves in (AC) present this as a ratio (non-dispersive/dispersive) for the case where dispersal responds to viability selection in a closed landscape. The dotted curve shows the same ratio when population regulation applies but viability selection does not, and the dashed curve shows this ratio when viability selection applies but population regulation does not. (A) shows these ratios early in the evolution of dispersiveness (mean(p_B) = 0.9) and (C) shows the ratios later on (mean(p_B) = 0.1). For reference, (BD) show the frequency of the *A* allele (open bars) and of *Ab* gametes specifically (black bars) early (mean(p_B) = 0.9) and late (mean(p_B) = 0.1) in the evolution of dispersiveness. Parameters: [v, σ, s, d_A, d_B, r, L, T] = [0.9, 0.3, 0.05, 0, 0, 0, 50, 20].

The fitness costs of dispersiveness that are associated with overcrowding dominate in patches where the non-dispersive *b* allele is prominent (indicated as dark bars in Fig. 4B) during the early stages of the evolution of dispersiveness (Fig. 4A). More dispersive individuals that express a movement preference tend to become aggregated on the edges of the transition zone where they face increased competition for opportunities to mate. Less dispersive individuals that remain in the transition zone have a better chance of reproducing successfully, even if they are less likely to survive to adulthood.

Figure 4C, D illustrates how the interplay between the fitness costs changes as evolution progresses. The overall fitness costs of dispersiveness become much weaker as the non-dispersive allele spreads (solid curve in Fig. 4C; note different axis scales in Fig. 4A and 4C). The relative importance of crowding effects also becomes much weaker and local

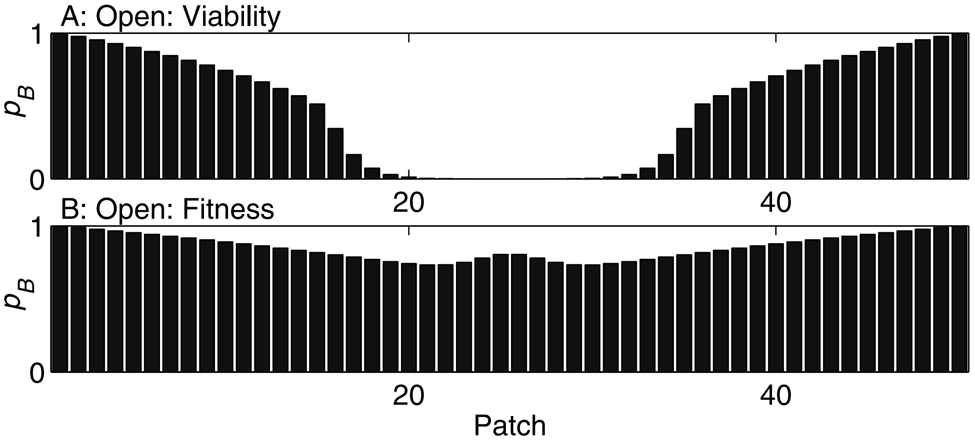

Fig. 5. *Spatial distribution of dispersiveness for directed movement in open landscapes.* Spatial distribution of dispersive B alleles in open landscapes in equilibrium for directed movement (A) in response to viability selection and (B) in response to fitness. Parameters: $[v, \sigma, s, d_A, d_B, r, L, T] = [0.6, 0.3, 0.05, 0, 0, 0.1, 50, 20]$.

adaptation starts to become relatively more influential. Were population regulation switched off altogether, strongly directional movement would actually confer a fitness advantage, because individuals climb the gradient in viability selection (dotted line indicates ratio of Ab offspring to AB offspring is less than 1). However, this advantage is nullified by population regulation because dispersing individuals face greater competition for mating opportunities (dotted and dashed curves oppose one another).

Open landscape

In the open landscape, dispersive individuals expressing a movement preference again become aggregated on the edges of the transition zone where they face increased competition, and non-dispersive individuals that remain in the transition zone enjoy greater opportunities for reproduction if they survive to adulthood. This crowding effect leads to a loss of dispersiveness and steepening of the cline (Figs. 2C and 3C) that progresses more quickly the more responsive dispersal is to the environment (larger v). For very responsive dispersal, this can result in dispersers abandoning the centre of the transition zone altogether (Fig. 5A), leaving a stepped cline at the A locus (dashed and solid curves in Fig. 3C). Across the whole landscape, however, a dispersal polymorphism results, because the loss of dispersiveness is held in check by the in-migration of dispersive individuals from the core populations (Figs. 2C, 5A).

Movement responds to expected fitness

When dispersers respond to both the gradient in juvenile survivorship and overcrowding by moving in response to their expected fitness, the initial clines at the A locus are steeper than they are when individuals respond to juvenile survivorship only. The clines are also steeper the more responsive dispersal is to the environment (left-hand side of Figs. 3B and D). If individuals find themselves on the side of the transition zone where they are maladapted, they once again have a strong preference for moving back across the transition to their preferred side of the landscape. However, they no longer continue to bias their movement out towards the very ends of the transition zone itself once on their preferred side. Instead, eventual overcrowding on their preferred side of the landscape and competition with equally well-adapted individuals leads pure types to push back into the transition zone. The solid line in Fig. 1A and inset illustrates this; the solid line shows the distribution of expected fitness ($w_{AA}/\bar{w}$) for an AA homozygote in the initial equilibrial cline that is attained by the end of the 5000 generation seeding phase of the simulations, before the introduction of the mutant b allele. The expected fitness of AA individuals reaches a small peak just to the left of the centre of the transition zone (solid curve in inset in Fig. 1A). Therefore, these individuals have a slight preference to move right as they approach the transition zone to escape overcrowding. [For more discussion of the structure of the basic clines, see Armsworth and Roughgarden (2008).] If the responsiveness of dispersal to the environment is increased, dispersal in response to expected fitness will eventually maintain a stepped cline.

Closed landscape

Directed movement in response to expected fitness tends to aggregate individuals in the centre of the transition zone itself, where they face increased competition. This cost to dispersal from exacerbating crowding effects is akin to that observed when dispersers respond to juvenile survivorship only, but is not as strong. Once again, this crowding effect results in an initial rapid spreading of the non-dispersive allele following its introduction, with the rate of spread being faster the more responsive dispersal is to the environment (left-hand side of Fig. 2B). More responsive movement once again though offers the long-term advantage of weakening indirect selection pressure and the rate of loss of dispersiveness eventually reverses, with dispersiveness being lost more slowly the more responsive dispersal is to the environment (right-hand side of Fig. 2B).

The spatial distribution of dispersiveness during its evolution is again more heterogeneous than for unresponsive movement. Predictably, dispersiveness is lost more slowly in the landscape edges. However, because dispersers tend to push into the very edges of the environmental transition zone, there is a small peak of dispersiveness in the transition zone itself (Fig. 1C).

These dynamics have important implications for the steepness of the cline at the A locus. The gene frequency cline at this locus is initially steeper the more responsive movement is to the environment. But, because indirect selection pressure is weaker and more dispersiveness is retained over the long term and because dispersive individuals remain clustered at the centre of the transition zone, a smooth cline can be maintained for longer with very responsive movement (Fig. 3B).

Open landscape

In the open landscape formulation, the initial costs associated with highly responsive movement subjecting individuals to overcrowding are once again sufficient to lead to some losses of dispersiveness (solid and dashed trajectories in Fig. 2D), even though indirect selection pressure alone is not (dotted trajectory in Fig. 2D). These losses eventually balance the in-migration of dispersers from the core populations and the dynamics equilibrate at a dispersal polymorphism once more. Because crowding effects are not as pronounced as they are when dispersal responds to juvenile survivorship only, a greater level of dispersiveness is retained in polymorphism this time (comparing Figs. 2C and D). The impacts of dispersal evolution are not sufficient to trigger major changes in the steepness of the cline at the *A* locus (Fig. 3D).

The dispersal polymorphism is spatially structured in a way that is similar to that for the closed landscape (Fig. 5B). There is a small peak of dispersiveness at the very centre of the transition zone, although there is a local deficit of dispersers in the wider transition zone. And dispersiveness is greatest towards the landscape edges where the influence of the strong selection for dispersal in core populations is felt most acutely.

Other parameters

- The qualitative results do not depend sensitively on the width of the transition zone and strength of selection gradient between adjacent patches.
- The qualitative results are also unchanged when assuming a smooth rather than piecewise linear selection gradient.
- The non-dispersive allele can only spread across the genetic background if there is some recombination. Thereafter, the rate of dispersal evolution decreases as r increases. See Billiard and Lenormand (2005) for more complicated roles that the recombination rate can play when the large population size assumption is relaxed.
- The non-dispersive allele can only spread across the landscape when it is not fully dominant ($d_B > -1$). But provided this is true, dispersal evolution progresses more slowly as d_B increases towards 1 and the non-dispersive allele becomes recessive.
- Finally, dominance at the *A* locus shifts the centre of the cline but does not affect the outcome of dispersal evolution or the dependence of cline steepness on different dispersal assumptions.

DISCUSSION

Dispersal incurs a range of costs and generates a range of benefits for an individual (Ronce, 2007). The relative importance of different costs and benefits depends on the specific details of dispersal behaviour (Armsworth and Roughgarden, 2005a, 2005b). Here, I examined a widely discussed cost of dispersal, namely that it can inhibit local adaptation in the presence of environmental gradients. Specifically, I focused on clines and local adaptation in gradual environmental transitions. Recent work has shown that the structure of clines depends sensitively on what is assumed about dispersal (Armsworth and Roughgarden, 2008). The present results go further and demonstrate what the implications of this are for the costs of dispersiveness.

The indirect cost of dispersal inhibiting local adaptation is weakened the more responsive dispersal is to environmental conditions, and may even be reversed for strongly directional movement. However, this comes at the expense of increasing other costs associated with dispersiveness, because more responsive directed movement tends to aggregate individuals in particular locations and increases the costs associated with overcrowding. The interplay between these two forces varies as evolution progresses, a result most clearly illustrated in the case of the closed landscape. Initially, the consequences of overcrowding are the more important, and, later on, it is the indirect costs arising from dispersal inhibiting local adaptation that dominate the dynamics.

While the study focuses on dispersal costs, the overall outcome of dispersal evolution also depends, unsurprisingly, on what is assumed about dispersal benefits. I compare two contrasting assumptions. In one (open landscapes), I assume strong selection maintains dispersal in core populations. In the other (closed landscapes), I examine the changing nature of the fitness costs of dispersiveness in isolation. By including the two assumptions, I compare both extreme scenarios. The open landscape models would probably represent a greater number of situations, albeit rather simplistically. A more sophisticated treatment would model the particular benefits and costs of dispersal in the core populations and transition zone simultaneously. The closed landscape formulation is arguably the more helpful for developing theoretical understanding of the evolutionary and ecological mechanisms at work, because it isolates the focal costs of dispersiveness and allows them to run their course before adding other, potentially confounding, factors.

The open and closed landscape models are finite, stepping stone analogues to different formulations of cline models in continuous space. Models that treat space as a continuous, infinite line commonly assume boundary conditions at infinity that have each locally favoured allele at fixation (Slatkin, 1973; May *et al.*, 1975). These boundary conditions are akin to our assumption in the open landscape models. The open landscape formulation allows us to examine the dynamics when evolutionary changes in the cline are constrained by evolutionary pressures elsewhere. Also relevant to our open landscape models therefore are models of the interplay between local adaptation and gene flow in continent–island systems (Haldane, 1930; Servedio and Kirkpatrick, 1997), and their extensions to finite stepping stone landscapes (Maruyama, 1970). However, other continuous space cline models consider finite domains and assume landscape boundaries are reflecting (Nagylaki and Moody, 1980). These boundary conditions provide the relevant analogy to the closed landscape models used here.

The choice between open and closed landscape formulations determines the long-term outcome of dispersal evolution. In open landscapes, dispersiveness is retained over the long term. The more responsive dispersal is to the environment, the less dispersiveness that is retained, because, of the two costs of dispersiveness, only overcrowding is strong enough to counteract the in-migration of dispersers. In the closed landscapes, dispersiveness is lost over the long term because the models only consider dispersal costs, with the rate of loss depending on how responsive dispersal is to the environment and changing as the balance of costs changes through time.

The other key contrast examined in the models is between dispersal that responds to some component of fitness only (juvenile survivorship) and dispersal that is fully fitness dependent. The former situation could arise if resources were not as limited as they are today when the species evolved its responses to dispersal cues, which has been termed an 'ecological trap' (Kokko and Sutherland, 2001; Robertson and Hutto, 2006). Many published models of responsive dispersal make this assumption (e.g. Cosner and Lou, 2003; Cantrell *et al.*, 2006). Model results make clear that the differences between the two dispersal assumptions matter for understanding how costs of dispersiveness change when dispersal is viewed as a phenotypic response to the environment. Both dispersal behaviours weaken the indirect cost dispersiveness incurs by counteracting local adaptation. However, dispersal in response to juvenile survivorship incurs greater additional costs from dispersal-induced overcrowding than dispersal in response to expected fitness. In essence, dispersal-induced overcrowding is more of an issue for the dispersal strategy that does not respond to population density. The crowding-related costs of dispersal in response to expected fitness could be lower still if I were to assume dispersal decisions for a cohort were distributed across a season. Then, dispersal decisions of late-dispersing individuals could reflect the emigration and immigration of early movers. Another clear difference in consequences of the two dispersal strategies concerns the spatial distribution of dispersive alleles. Dispersers leave the transition zone when dispersal responds to juvenile survivorship only, but aggregate there when it responds to expected fitness.

Finally, both sets of comparisons, closed versus open landscapes and whether dispersal responds to juvenile survivorship or expected fitness, matter when trying to understand the consequences of dispersal evolution for the cline at the selection locus. In open landscapes, the continual influx of dispersers is sufficient to always maintain a gradual cline at the A locus, except in the perhaps artificial case of very responsive movement in response to viability selection. In closed landscapes, the reverse prediction is true and partially responsive dispersal in response to juvenile survivorship or highly responsive dispersal in response to expected fitness are key to maintaining gradual clines over the long term.

Assumptions and extensions

The models of dispersal evolution show that indirect selection pressure against dispersal is ameliorated for more complex dispersal behaviours, although this can come at the expense of other costs of dispersiveness resulting from overcrowding. However, on their own these costs will not determine the overall outcome of dispersal evolution. Instead, these costs will act in concert with a range of other factors (Ronce, 2007). The models do not yet incorporate temporal variation in fitnesses. But for many systems, the benefits of dispersal may only become apparent when accounting for temporal variation in the environment (reviewed in Armsworth and Roughgarden, 2005b). Studies that embed temporal variation into spatially extended cline models are unavailable even for unresponsive dispersal. Two-patch models suggest that evolutionarily stable dispersal strategies for different dispersal behaviours depend on environmental autocorrelation (Doligez *et al.*, 2003; Armsworth and Roughgarden, 2005a, 2005b) and what is assumed about population regulation (Armsworth and Roughgarden, 2005a, 2005b).

As is common in cline studies and many classic writings on the evolution of dispersal, I have treated the gamete frequencies as being continuously distributed and studied the deterministic approximations of what are, ultimately, stochastic evolutionary processes. Interpreted literally, this is equivalent to assuming local population sizes are infinite. But the more relevant statement is that continuum formulations of this type have proved very influential for understanding evolutionary processes in clines. The obvious disadvantage to such assumptions is that they preclude study of kin competition and inbreeding. Billiard and Lenormand (2005) recently examined the interaction between kin competition and inbreeding and local adaptation in determining the outcome of dispersal evolution in a two-patch metapopulation with unresponsive dispersal. The authors found that adaptation effects of the type studied here played a dominant role over much of parameter space for larger populations (deme sizes of greater than 100 individuals or so), although the ultimate outcome of dispersal evolution was retention of a small but positive amount of dispersiveness.

I also ignored additional, direct costs of dispersal in the models. Direct dispersal costs can arise through increased mortality during dispersal (Hanski *et al.*, 2000) or because dispersal traits come at the cost of reduced juvenile survivorship or fecundity (Singer and Hanski, 2004). Information collection can itself be costly (Stamps, 2001), which would impact species heavily dependent on information acquisition (high v).

I kept the genetic assumptions simple. Model extensions that recognize the traits in question will often be under the control of many loci would also be worthwhile [but see Roff and Fairbairn (1991), Caillaud *et al.* (2002) and Haag *et al.* (2005) for examples where a small number of loci appear to be involved in determining dispersiveness]. I assumed a linear selection gradient to allow ready comparisons with other published work. The results are not sensitive to repeating the analyses assuming a smooth transition in viability selection, one that avoids the 'corners' or 'joins' in the linear functional form. I also kept the assumptions about population dynamics very simple. The strength of indirect selection in spatially extended cline models depends on population size gradients, which can lead to asymmetric gene flow from larger core populations into smaller, peripheral ones (Garcia-Ramos and Kirkpatrick, 1997; Alleaume-Benharira *et al.*, 2006). However, the results are largely unchanged when I re-ran the models but assumed a 50% reduction in population density in the centre of the transition zone.

CONCLUSION

Related work has shown that the shape of clines depends on the specifics of what is assumed about dispersal behaviour (Armsworth and Roughgarden, 2008). Here, I have extended this work to demonstrate in turn how the indirect costs of dispersing in transition zones also depend on the specific details regarding dispersal, which has implications for the permanence of clines, the integrity of species, and for the spatial distribution of dispersiveness. As has been shown to be the case with other costs and benefits of dispersal (Armsworth and Roughgarden, 2005a, 2005b), the extent to which particular costs are realized depends very much on the specific detail of how organisms disperse. This reiterates the need for further empirical studies of dispersal *in situ* in environmental transition zones. Perhaps contrary to initial expectation, it is not the case that more responsive movement is less costly than unresponsive dispersal. Rather, the particular costs that prove most important and the evolutionary implications of these costs are different with responsive movement.

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APPENDIX

To illustrate the indirect costs of dispersiveness, I compared the number of copies of itself an A allele successfully propagated through into the next generation when it was combined into an AB gamete in the previous generation and when it was combined into an Ab gamete. To simplify the illustration, I focused on the case where there was no recombination ($r = 0$). I counted the number of copies left by each gamete type among pre-dispersal genotypes in the next generation to allow time for dispersal to affect both overcrowding and local adaptation. I presented the results as a ratio of Ab offspring to AB offspring. The numerator of the relevant ratio (copies left by an Ab gamete) is

$$\sum_{m=i-1}^{i+1} \left(\frac{[\sigma_{mi} w_i]_2 [w_m]_2}{\displaystyle\sum_{j=m-1}^{m+1} \sum_{k=1}^{4} [\sigma_{mj} w_j]_k x_{jk}(t)} \right), \tag{A1}$$

where the new index m is summing over the destination patches into which the offspring of a parent initially located in patch i can be born. The denominator of the ratio (copies left by an AB gamete) looks similar but the relevant marginal fitnesses and dispersal-weighted marginal fitnesses are computed for the AB gamete; i.e. the subscripts indexed as 2 in equation (A1) are replaced with subscripts indexed 1 to indicate the relevant gamete type.

To compare the overall fitness costs with the effects of viability selection acting in isolation, the double summation term making up the denominator in equation (A1) is ignored. And to compare both of these sets of costs with those associated with the effects of population regulation acting in isolation, the marginal fitnesses in the numerator of equation (A1) (the $[w_m]_2$ terms) are omitted.