

# Local adaptation in dispersal in multi-resource landscapes

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The distribution of resources in space has important consequences for the evolution of dispersal-related traits. Dispersal moderates patterns of gene flow and, consequently, the potential for local adaptation to spatially differentiated resource types. We lack both models and experiments that evaluate how dispersal evolves in landscapes with multiple resources. Here, we investigate the evolution of dispersal in landscapes that contain two resource types that differ in their spatial autocorrelations. Individuals may possess ecological traits that give them a fitness advantage on one or the other resource. We find that resources differing in their spatial autocorrelation select for different optimal dispersal strategies and, further, that some multi-resource landscapes can support the stable coexistence of distinct dispersal strategies. Whether divergence in dispersal strategies between resource specialists occurs depends on the underlying structure of the resources and the degree of linkage between dispersal strategies and ecological specialization. This work indicates that the spatial autocorrelation of resources is an important factor in determining when evolutionary branching is likely to occur, and sheds light on when secondary isolating mechanisms should arise between locally adapted specialists.

**KEY WORDS:** Competition, divergence, migration rate, movement, polymorphism, spatial autocorrelation.

A major challenge in evolutionary biology is understanding how complex landscapes influence phenotypic evolution. In nature, resources vary in type and abundance across space and time. How an organism responds to this variation will depend on the process of dispersal. Increased rates of dispersal are thought to evolve so that individuals can minimize kin competition, reduce the likelihood of inbreeding, and mitigate the negative consequences of spatial and temporal variability in resources (Frank 1986; Duputié and Massol 2013). Past work on this third factor has greatly improved our understanding of how dispersal evolution should proceed in landscapes that contain a single resource (Heino and Hanski 2001; Bonte et al. 2010; Henriques-Silva et al. 2015). However, we do not completely understand how dispersal should evolve in landscapes that contain multiple resources. Unlike single resource landscapes, the presence of multiple resources creates opportunities for specialization to both the type of resource and to the arrangement of resources in space. In

addition, because competition between specialized phenotypes (i.e., those that are better able to exploit one resource over another) has the potential to alter the way individuals experience a landscape, dispersal evolution may proceed differently than when the landscape comprises only a single resource.

Theory for dispersal evolution typically focuses on the effects of spatial or temporal variation in a single resource type (Heino and Hanski 2001; Hovestadt et al. 2001; Travis 2001; Bonte et al. 2010; Massol et al. 2010; North et al. 2011; Snyder 2011; Henriques-Silva et al. 2015) and does not integrate local adaptation to multiple resource types (but see Berdahl et al. 2015). Past theory that has investigated the evolution of function-valued dispersal traits in spatially explicit landscapes, but without spatial heterogeneity, has found that the shape of the evolved dispersal kernels reflects the trade-off between kin competition and costs associated with dispersal distance (Rousset and Gandon 2002). Spatial heterogeneity in resource availability alters the mortality

costs of dispersal, and can act as an important selective force on both the probability of dispersal and dispersal distance (Hovestadt et al. 2001).

In parallel, work on local adaptation rarely accounts for how resources are clustered in space (as highlighted in Richardson et al. 2014). Although dispersal and its role in gene flow is known to be of vital importance for the maintenance of local adaptation (Bolnick and Nosil 2007; Alzate et al. 2017; Pederson et al. 2017), evolution of dispersal has remained widely ignored in this literature. The few studies that do integrate local adaptation with dispersal evolution use highly simplified or spatially implicit landscapes (e.g., Kisdi 2002; Billiard and Lenormand 2005; Berdahl et al. 2015), restricting inference to a small set of systems.

Local adaptation is broadly defined as a pattern in which resident genotypes in a particular habitat type have a fitness advantage over genotypes arriving from other habitat types (“local vs. foreign”; Kawecki and Ebert 2004). Local adaptation arises when there is a fitness trade-off, such that genotypes with high fitness in one habitat have lower fitness in alternative habitats. This trade-off, which we will refer to as “specialization,” results in local adaptation when specialist genotypes are spatially associated with the habitat where they have their highest fitness. Whether or not this spatial association arises depends on the strength of specialization and the rate of gene flow between habitat types, which is itself a function of dispersal and the spatial structure of the habitat. Strict definitions of local adaptation consider only spatially separated habitats and, therefore, make no assertions about how genotypes might interact in locations where both habitat types co-occur. Such locations cannot display “local adaptation” to one habitat type, but their ability to support multiple types of specialists might make them sites for increased gene flow between specialists.

There are numerous examples of local adaptation to different resources in nature and it is clear that different resources rarely exhibit identical spatial distributions. For example, there are many cases of plant-feeding insects that are specialized on different host plants that differ in their spatial abundance and autocorrelation. Some host plants, like those grown for agriculture (e.g., apples, host to the apple-maggot fly; Bush 1969) or as ornamentals (e.g., golden rain tree, host to soapberry bugs; Carroll and Boyd 1992) will commonly occur in large dense clusters, while their wild counterparts are likely to be less abundant and/or clustered. In the case of the red-shouldered soapberry bug, local adaptation between the ornamental golden rain tree and a native balloon vine has resulted in divergence in dispersal morphology (Carroll et al. 2003), but the reasons for this divergence remain unclear. To understand these systems, models and experiments are needed that investigate the interaction between local adaptation and the evolution of dispersal in spatially heterogeneous landscapes.

Specialization can influence the evolution of dispersal by restricting where individuals persist on the landscape, either by reducing fitness on some resource types or by mediating competition between specialists (Shenbrot et al. 2007). In parallel, dispersal influences the distribution of specialist genotypes, which determines both the potential for gene flow between populations and the spatial scale of competition (Lenormand 2002). How these processes will interact is not obvious and, thus, necessitates the development of new theory.

In nature, specialists that are adapted to different resources can arise via divergent selection (e.g. Nosil 2004; Toju 2009). If the spatial distributions of the resources overlap, then we might expect specialists to compete in locations where both resources co-occur, provided that competition is also influenced by other factors. For example, if a bird species contains specialists on large and small seeds and plants producing those seeds co-occur in space, those specialists may compete for territories, nesting materials, or secondary food resources; experience apparent competition due to predation; or be jointly regulated by disease, even if they do not directly compete for seeds. Resultant competition may lead to specialist species inhabiting only a subset of the patches containing the resource they are specialized on. In ecological terms, the presence of a competitor may lead to each specialist occupying a “realized spatial niche” that differs from its “fundamental spatial niche.” Because the landscape a species actually inhabits is a key factor that determines how dispersal evolves, a change in the realized spatial niche due to competition may change the evolutionary trajectory of dispersal-related traits.

In spatial models, which specialist is competitively dominant in a patch will depend not only on the type and abundance of resources in that patch, but also on the rates of immigration and emigration of each specialist. One specialist may dominate an area where it does not have a local advantage simply because it has a higher rate of immigration. As a result, a specialist may dominate patches of any habitat type that occur in regions where that specialist is locally abundant. In general, we might expect specialists that evolve higher dispersal rates to dominate locations where no specialist has a fitness advantage (e.g., patches containing both resources in equal proportion), potentially creating an eco-evolutionary feedback between dispersal propensity and the fraction of the landscape a specialist occupies. For example, if a highly dispersive specialist displaces a less dispersive specialist in patches where both species co-occur, the less dispersive species may become restricted to smaller and more remote patches. Such isolation may itself select for further reductions in dispersal propensity in those populations.

In this article, we use individual-based simulations in spatially explicit, two-resource landscapes to address four primary aims. (1) We test whether previous findings for single-resource landscapes hold in multi-resource landscapes. (2) We

incorporate resource specialization to assess when polymorphic dispersal strategies will arise. (3) We include a genetic association between dispersal and specialization loci and ask whether the effects of linkage on dispersal evolution are influenced by the spatial distribution of resources. (4) We ask how the strength of ecological specialization influences patch occupancy and competition and assess the effects on the evolutionary trajectories for dispersal strategies.

## Methods

We develop a simulation model in which individuals are situated across a two-dimensional lattice of connected patches. The patches in this “landscape” may contain one or both of two possible resources, or no resources at all. The individuals that inhabit these patches are haploid and characterized by two traits: a dispersal kernel and an ecological specialization. Ecological specialization traits are alleles that confer resource-specific fitness. Each generation begins with patch disturbance, followed by dispersal, natural selection on ecological traits, and growth (reproduction and density regulation), in that order. This is similar to the adult dispersal life cycle described by Massol and Débarre (2015). We describe each of these processes in greater detail below. For parameter symbols and values, see Table 1.

### LANDSCAPES

We construct landscapes using a  $128 \times 128$  grid. We assume that two adjacent patches in the lattice are a unit distance away from one another. Each patch in the landscape is either uninhabitable (contains no resources) or contains either or both of two resources which we denote *A* and *B*. Resources *A* and *B* are distributed across the landscape with spatial autocorrelations  $\sigma_A$  and  $\sigma_B$  and each occupies some fraction of the total available patches in the landscape, denoted  $f_A$  and  $f_B$ , respectively (Fig. 1). We generate landscapes using the methods described in Haller et al. (2013), where our  $\sigma$  corresponds to their parameter  $l_g$  (and other parameters were  $s = 0$ ,  $c = 0$ , and  $a = 1$ ; see Haller et al. 2013 for details). Landscapes generated using this method are characterized by continuous values within each cell; we discretized the landscape by setting patches above and below a given threshold to 1 and 0, respectively. We chose the threshold in each case to obtain the required fraction of habitable patches. We confirmed that this method created appropriate low, moderate, and high autocorrelation landscapes using Moran's *I*, a metric for calculating spatial autocorrelation in discrete landscapes on a lattice. Landscapes with no spatial auto correlation have a Moran's *I* of 0, while maximally autocorrelated landscapes have a Moran's *I* of 1. Here, we chose spatial autocorrelation values of  $\sigma = 0.001, 0.01$ , and  $0.1$  to generate landscapes. These

correspond to Moran's *I* values of approximately 0.32, 0.65, and 0.96, respectively, when  $f = 0.3$ . Therefore, our chosen values of  $\sigma$  effectively span a range of low (but nonzero) to high levels of spatial autocorrelation in our discrete landscapes.

Each resource is independently distributed: the presence of one resource has no influence on the presence of the other. Therefore, the number of habitat patches containing both resource types together does not depend on the spatial autocorrelation of either resource. New landscapes were randomly generated using the same  $\sigma$  and  $f$  values for each replicate.

### DISTURBANCE

Landscapes are initialized with each patch at carrying capacity (described below). Each generation, patches independently experience disturbance events with probability  $d$ . A disturbance event in a patch kills all individuals inhabiting the patch. Disturbance does not change patch quality and patches can be immediately recolonized.

### DISPERSAL

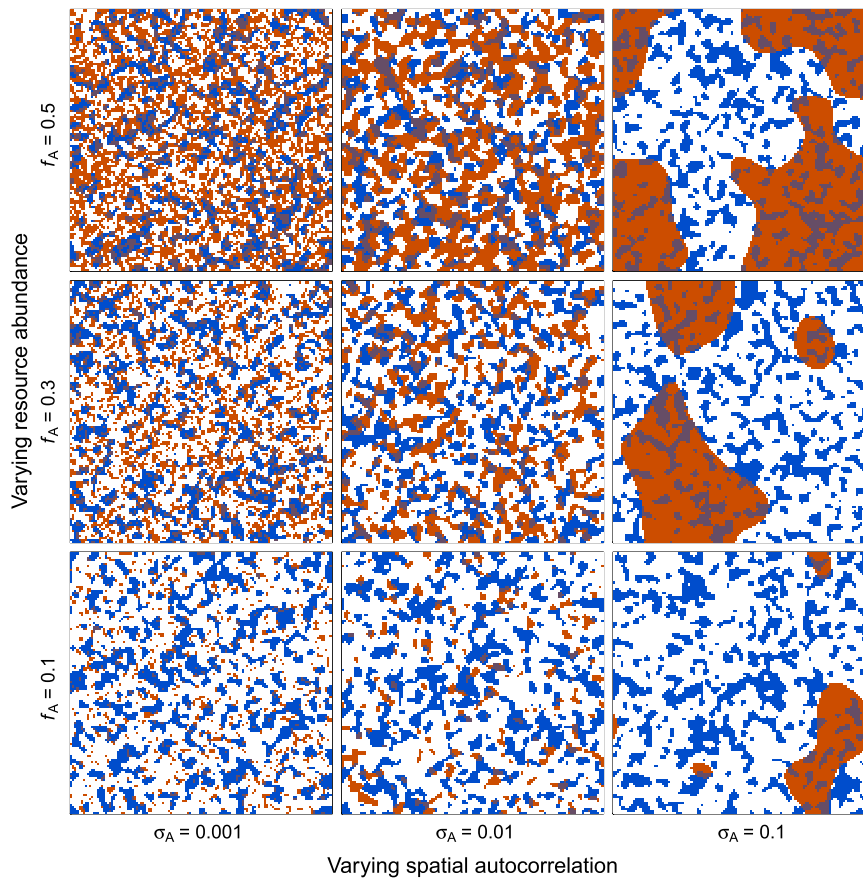
An individual's dispersal kernel is a “function-valued trait” (e.g., see Dieckmann et al. 2006) that comprises a fixed number of probabilities ( $k$ ), where the  $i^{\text{th}}$  value denotes the probability that that individual disperses to a patch whose distance from the natal patch lies in the interval  $(i - 1, i]$  (note that the value for  $i = 0$  denotes the probability that an individual does not disperse). An individual's dispersal distance is then drawn from its dispersal kernel and it disperses to a patch that distance away in a random direction; note that distances to patches that are not along the cardinal axes are discretized in order to accomplish this (Fig. 2). The first bin in an individual's dispersal kernel corresponds to a dispersal distance of zero; therefore, individuals do not necessarily disperse away from their natal patch. Because dispersal direction is random, individuals land in uninhabitable patches or patches of the wrong resource type in proportion to the frequency of those patch types at each distance class  $i$ . Dispersal beyond landscape boundaries is wrap-around. Populations are initialized with a single dispersal type with a kernel defined such that dispersal probability is uniformly distributed across the first 5 bins (but results remain qualitatively the same using alternative starting conditions; see Fig. S1).

### SELECTION

Individuals occupying habitable patches will survive with probability  $w_{i,j}$ , which is determined by their ecological specialization allele,  $i$ , and the resource present in the patch,  $j$ . In patches with multiple resources, individuals experience their maximum survival probability. We denote ecological specialization alleles by  $a$  and  $b$  for *A*-adapted and *B*-adapted, respectively. We then define the strength of specialization,  $s_i$ , as the difference in survival

**Table 1.** Model parameters and model variables.

Symbol	Model parameter	Values tested	Default value
$f_j$	fraction of the landscape that is resource $j$	0.1,0.3,0.5	0.3
$\sigma_j$	spatial autocorrelation of habitat $j$	0.001,0.01,0.1	0.01
$\delta$	patch disturbance probability	0.1	0.1
$k - 1$	maximum dispersal distance	10, 20, 30	10
$w_{i,j}$	fitness of genotype $i$ in habitat $j$	0.5,0.95,1	1
$s_i$	strength of specialization in genotype $i$	0, 0.05, 0.5	0
$r$	maximum growth rate	1.01	1.01
$K$	patch carrying capacity	10, 100	10
$\psi$	recombination rate	0,0.1,0.5	0
$\mu$	mutation rate at ecological specialization locus	$1 \times 10^{-4}$	$1 \times 10^{-4}$

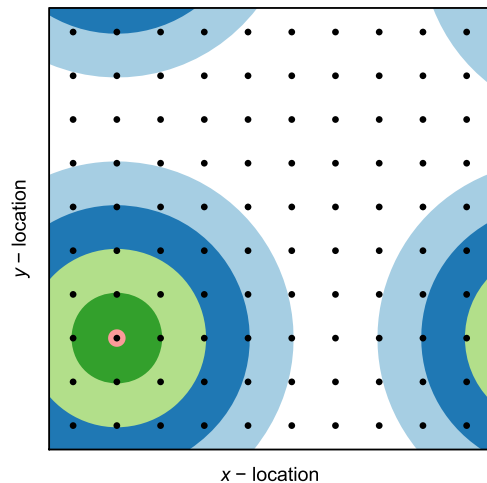


**Figure 1.** Sample landscapes with varying levels of spatial autocorrelation (for resource A [red],  $\sigma_A$  equals, from left to right, 0.001, 0.01, and 0.1; for resource B [blue],  $\sigma_B$  equals 0.01 in all panels) and abundance (for resource A,  $f_A$  equals, from top to bottom, 0.5, 0.3, and 0.1; for resource B,  $f_B = 0.3$  in all panels).

between the “best” habitat and the “worst” habitat for genotype  $i$ . In genotype  $a$ ,  $s_a = 1 - w_{a,B}/w_{a,A}$  and in genotype  $b$ ,  $s_b = 1 - w_{b,A}/w_{b,B}$ . High values of  $s_i$  indicate that specialization is strong and low values that it is weak. For ease of interpretation and to focus on scenarios where coexistence is probable, we restrict our application of the model to cases where specialization is symmetrical (i.e., where  $s_a = s_b$ ), recognizing that there may be interesting dynamics when this assumption is relaxed.

## REPRODUCTION

After dispersal and selection, individuals reproduce with patch-specific birth rates calculated using a logistic model with maximum growth rate,  $r_0$ , and patch carrying capacity,  $K$ . Reproduction is stochastic: the number of offspring each individual produces is drawn from a Poisson distribution with a mean of  $1 + r_0 * (1 - N/K)$ , where  $N$  is the population size in their local patch. Thus, population regulation happens at the patch level



**Figure 2.** A diagram to illustrate how dispersal steps of various distances are implemented in our landscape. Each concentric ring represents a potential dispersal distance (in this case,  $k = 5$ ), and each point on the grid indicates the center of a patch. If a disperser begins from the pink location on this diagram, the dark green circle indicates patches where  $i = 1$ , the light green circle where  $i = 2$ , etc. Because dispersal direction is random in our model, every patch within a distance class is equally likely.

and is simultaneous with reproduction. We focus on cases with  $K = 10$  here, but our results are qualitatively similar for higher  $K$  (see Fig. S2).

Individuals are hermaphroditic and haploid and, thus, offspring inherit the complete genotype of one parent unless there is recombination or mutation. We assume that genetic associations between alleles underlying the two traits are broken apart by recombination with probability  $\psi$ . That is,  $\psi$  is the probability that an individual receives its ecological specialization allele and its dispersal allele from different parents. The number of recombinant genotypes arising in each patch will therefore depend on both the frequency of  $a$  and  $b$  individuals and the value of  $\psi$ . Free recombination and random mating occur when  $\psi = 0.5$ . Because assortative mating and physical linkage would each generate disequilibrium between the ecological specialization and dispersal loci, we will refer here only to the rate of recombination,  $\psi$ , realizing that such a parameter could also be adjusted to describe the degree to which mating is random.

Both ecological specialization alleles and dispersal traits may undergo mutation during reproduction. Ecological specialization alleles mutate from  $a$  to  $b$  and vice versa with probability  $\mu$ . To model mutation of the dispersal kernel, we follow the methods presented in Hovestadt et al. (2001). Namely, to create a mutant, two bins from the mutant parent's dispersal kernel are randomly selected and a fraction of the probability from one bin is moved to the other bin. This creates mutants that are identical to the parent in their dispersal probability to all but two distance classes.

Mutational effect sizes were randomly generated for each mutation event with the limitation that the amount of probability in a bin could not be reduced by more than 90% by a single mutation. This limitation was imposed to reduce the occurrence of bins of extremely low, but non-zero, probability. This method creates mutants that are phenotypically similar to their parents and can generate kernels of any shape. The continuous nature of these probabilities means that the dispersal kernel can take an infinite number of possible states; for computational efficiency, we limit the total number of unique dispersal kernels segregating in the population at one time to 50, adding new mutants only when the number falls below that. We find no qualitative effects of the number of segregating mutants on our results (see Fig. S3 for example cases with 10 and 100 segregating mutants).

## EVALUATING SIMULATION OUTPUT

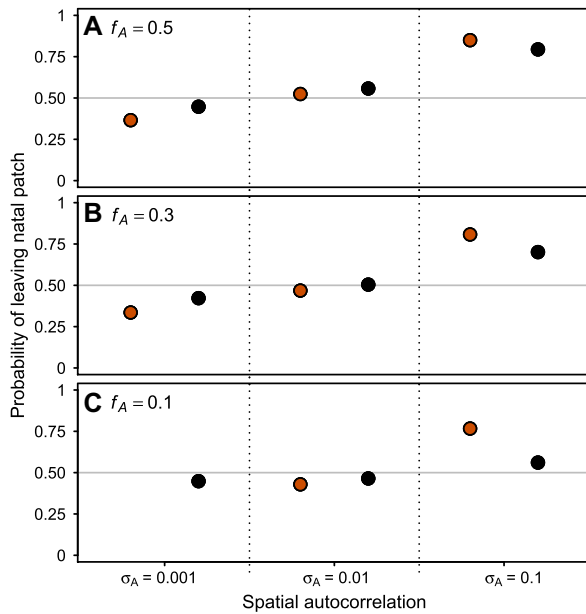
In order to evaluate how landscapes containing two resources differ from landscapes containing only a single resource, we make two types of comparisons:

1. With only a single specialist species (i.e., only a single ecological specialization allele), we compare the evolution of dispersal kernels in a landscape that contains one resource ( $A$ ) to a landscape that contains two resources ( $A$  and  $B$ ). To isolate the effect of adding a second resource, we compare each single resource landscape to the exact same simulated landscape with a second resource added. In addition, the single resource cases allow us to reproduce results from earlier work conducted on similar single resource landscapes.
2. We compare evolution in landscapes containing one specialist to those with two specialists. This allows us to isolate the potentially interacting effects of specialization strength and competition between specialists. In these comparisons, we quantify how competition influences the spatial distribution of each specialist (e.g., by comparing the abundances of each specialist in patches with either or both resource types). To make the most direct comparison, we use the same landscapes in simulations with one specialist and two specialists. We then evaluate how changes in occupancy as a consequence of competitive interactions influence the evolution of dispersal kernels.

## Results

### INCREASING SPATIAL AUTOCORRELATION INCREASES DISPERSAL PROBABILITY

We find that greater spatial autocorrelation favors increased dispersal in landscapes with a single resource ( $A$  in Fig. 1; red points in Fig. 3), which is consistent with earlier work (Hovestadt et al. 2001; Snyder 2011). We also find that increasing the fraction



**Figure 3.** Population mean probability of leaving the natal patch in landscapes with one (red) or two (black) resource types. Red points show means across 100 unique landscapes containing only resource *A*, while black points show means across the same 100 landscapes when resource *B* (blue) is added. (A), (B), and (C) show different abundances of resource *A*; spatial autocorrelation increases along the x-axis from left to right. Note that populations never persisted in single resource landscapes in the bottom left. All parameters but  $\sigma_A$  and  $f_A$  used the default values shown in Table 1.

of usable habitat leads to slight increases in the probability of dispersal (compare A, B, and C in Fig. 3).

Adding a second resource of intermediate spatial autocorrelation (*B* in Fig. 1) has the overall effect of increasing resource abundance on the landscape (from  $f_A$  to  $f_A + f_B - f_A * f_B$ ) and creating a mixed spatial autocorrelation. The overall autocorrelation is distinct from either  $\sigma_A$ ,  $\sigma_B$ , or the weighted mean of the two, but rather creates spatial heterogeneity in the  $\sigma$  individuals experience across the landscape. In the absence of ecological specialization ( $s_a = s_b = 0$ ), the addition of a second resource does not introduce any differences in individual survival between resources. Thus, any resultant differences in evolved dispersal kernels are solely a consequence of changes in the spatial structure of the landscape.

In landscapes with a second resource, evolved rates of dispersal are intermediate between those that would evolve on each resource in isolation (black points in Fig. 3). When both resources have the same  $\sigma$ , there is little effect of adding a second resource on dispersal evolution (Fig. 3, middle column), and the minor difference is likely a consequence of the increase in overall resource abundance. When resources differ in their spatial autocorrelation, the exact dispersal probability depends on both the total spatial

autocorrelation of both resources and their relative abundance; this trend is particularly pronounced when overall spatial autocorrelation is high (e.g., right column of Fig. 3). Interestingly, this is not because all individuals across the landscape are evolving the same intermediate dispersal kernel but, instead, because individuals are evolving dispersal kernels that are adapted to the spatial distribution of patches containing one resource or the other (Fig. 4). We will refer to this stable coexistence of distinct, spatially clustered dispersal strategies on the landscape as “divergence.”

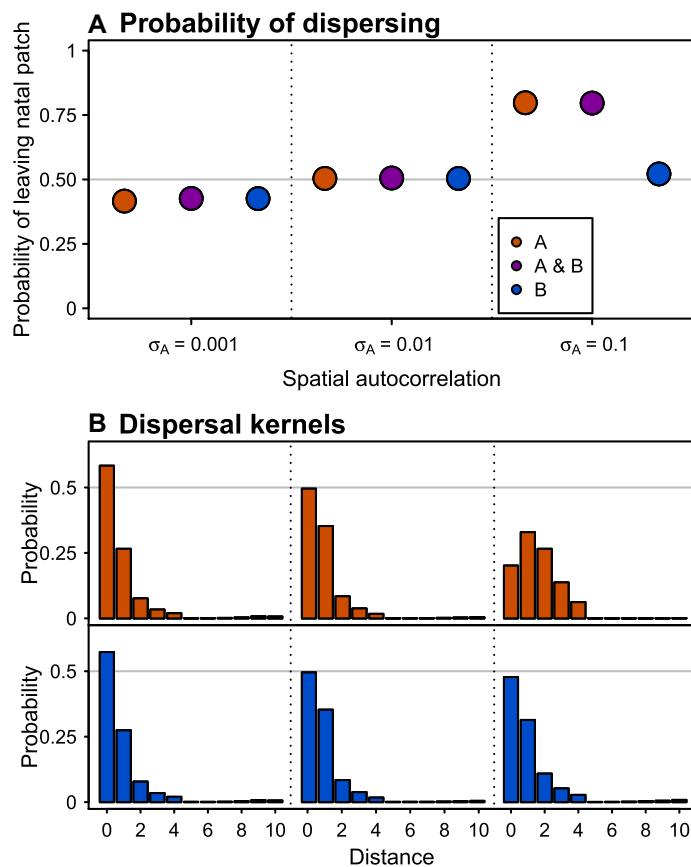
### HIGH SPATIAL AUTOCORRELATION PROMOTES DIVERGENCE

Even in the absence of ecological specialization ( $s_a = s_b = 0$ ), divergence in dispersal kernels can arise when spatial autocorrelation is high (Fig. 4A). When dispersal kernels diverge, this pattern is most striking in the first bin (the probability of remaining in the natal patch; Fig. 4B) and, consequently, we focus our discussion on patterns of divergence in this probability. Whether or not populations inhabiting different resources evolve divergent dispersal strategies depends on the absolute amount of spatial autocorrelation of the resources. When levels of spatial autocorrelation are high *and* differ between resource types, there is local variation on the landscape in both the cost of dispersal (from landing in a patch with no resources) and the benefit of dispersing to a suitable patch that is below carrying capacity. Patches of resources with low spatial autocorrelation will tend to be refilled more slowly because, on average, they have fewer habitable neighboring patches. These spatially varying selection pressures cause populations inhabiting patches containing different resource types to evolve different dispersal strategies, even in the absence of ecological specialization (Fig. 4,  $\sigma_A = 0.1$ ). When spatial autocorrelation is low, however, dispersal strategies do not diverge between resource types, even if one resource exhibits significantly higher autocorrelation than the other (Fig. 4,  $\sigma_A = 0.001$ ).

### ECOLOGICAL SPECIALIZATION EXPANDS THE CONDITIONS FOR DIVERGENCE

Ecological specialization expands the conditions under which dispersal strategies diverge between resources. With ecological specialization, divergence in dispersal strategies also occurs in landscapes with low spatial autocorrelation (compare  $\sigma_A = 0.001$  in Fig. 5 and Fig. 4). In addition, for landscapes with high resource spatial autocorrelation, specialization increases the strength of divergence (compare  $\sigma_A = 0.1$  in Fig. 5 and Fig. 4). This is true whether specialization is strong ( $s_a = s_b = 0.50$ ; Fig. 5) or weak ( $s_a = s_b = 0.05$ ; Fig. S4).

We expect divergence in dispersal strategies between ecological specialists to be favored when (1) selection on dispersal differs between resources; (2) there is a consistent association



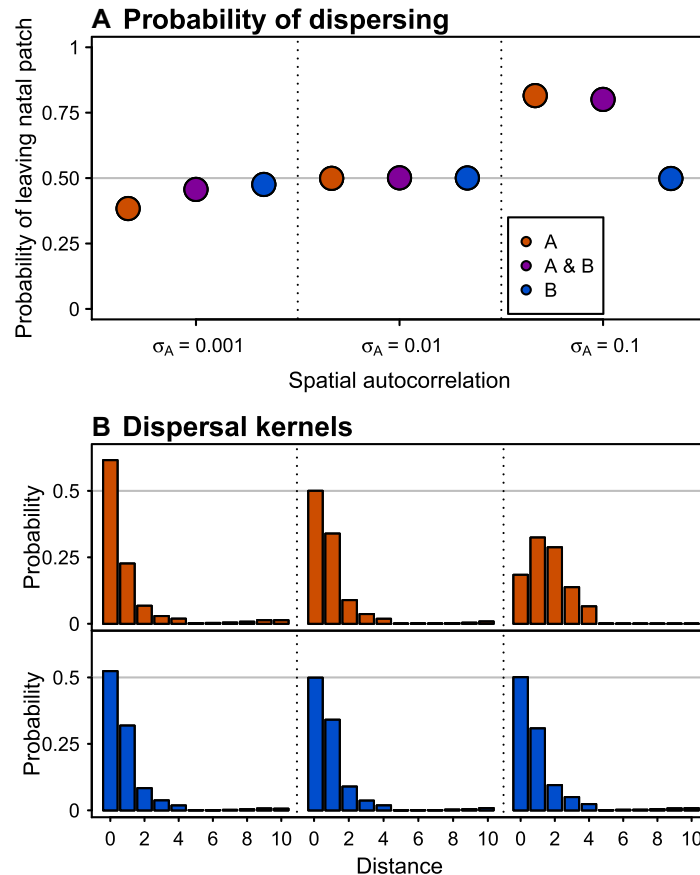
**Figure 4.** The evolved steady state for dispersal probability after  $2 \times 10^5$  generations for individuals inhabiting patches containing each resource type, without ecological specialization ( $s_a = s_b = 0$ ). (A) The population mean probability of leaving the natal patch in landscapes containing resources A and B together, with point color indicating patch type. Means are calculated separately for inhabitants of patches containing only resource A (red); only resource B (blue); or both resources together (purple). (B) Final dispersal kernels, with each bar indicating the probability that an individual will disperse to a patch within a given distance class. Mean kernels are calculated separately for inhabitants of patches containing only resource A (red) or only resource B (blue). Means in each panel are from runs across 100 unique landscapes. All parameters but  $\sigma_A$  held the default values shown in Table 1.

between ecological specialist genotypes and the resource type they are specialized on; and (3) opportunities for gene flow between patches containing each resource type are rare. The first condition is met whenever resources differ in their spatial autocorrelation, as evidenced by previous work (Hovestadt et al. 2001) and in our model on landscapes with only a single resource type (see above section, *Increasing spatial autocorrelation increases dispersal probability*). The second condition is met when individuals occur more often in patches containing their highest fitness resource than in patches without it. There are two processes that can cause this spatial association: (i) Specialists do not survive well in patches containing only low fitness resources, and/or (ii) Dispersal between patches containing the same resource type is more likely than dispersal between patches containing different resource types. This second process does not require specialization on different resource types and is most common in landscapes where at least one resource is highly spatially autocorrelated. The

third condition, that gene flow between resource types is low, can be satisfied either by spatial isolation (in the absence of ecological specialization), by individuals mating assortatively, or via minimal recombination between the ecological and dispersal loci. Opportunities for mating between distinct genotypes and recombination will only occur when specialists co-occur in space. We return to this later.

#### COMPETITIVE EXCLUSION PROMOTES DIVERGENCE IN DISPERSAL STRATEGY WHEN SPECIALIZATION IS WEAK

We find that divergence in dispersal strategy between populations inhabiting different resource types arises whenever there is some degree of ecological specialization. However, the mechanism driving divergence is not the same when specialization is strong and when it is weak. When specialization is strong, each specialist experiences high mortality on the “wrong” resource



**Figure 5.** Population mean probability of leaving the natal patch in landscapes with ecological specialization ( $s_a = s_b = 0.5$ ). Panels are otherwise as described in Fig. 4.

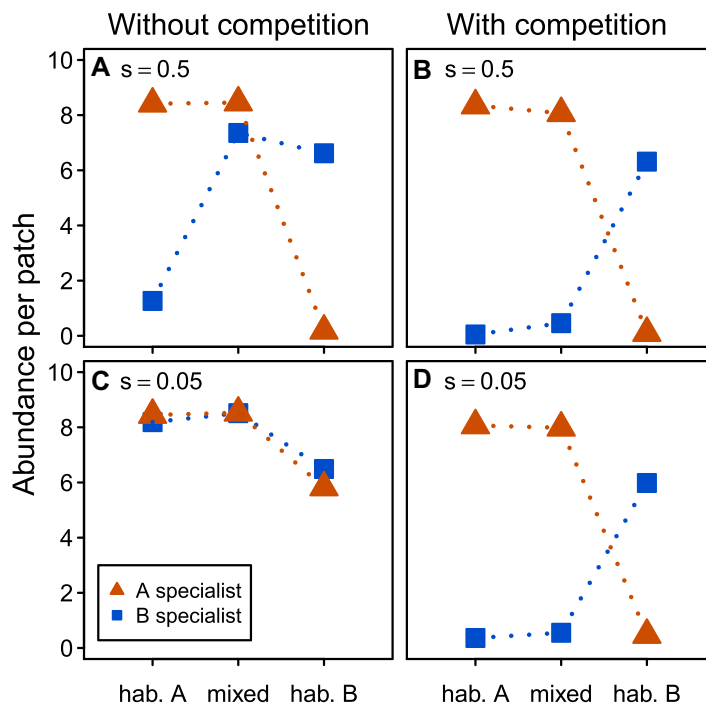
type and thus rarely occurs in patches of that resource, regardless of whether or not a competitor is present (Fig. 6A and B). Each specialist should, therefore, evolve a dispersal strategy that is best suited to the spatial distribution of its high fitness resource. In contrast, when specialization is weak, each specialist has high enough survival on the “wrong” resource to persist on that resource in the absence of competition; however, in the face of competition, that specialist may become spatially restricted via competitive exclusion to only its “best” resource (compare C and D of Fig. 6). Thus, in the absence of competition, each specialist should evolve a dispersal kernel adapted to the combined distribution of both resources but, with competition, selection should favor resource-specific optima.

These findings indicate that competition combined with weak specialization can mimic the effects of strong specialization and drive evolutionary divergence in dispersal strategies. However, this is not true when spatial autocorrelation is low: in this case, competition does not effectively produce spatial separation (Fig. S5) and thus, divergence, when present, is minimal.

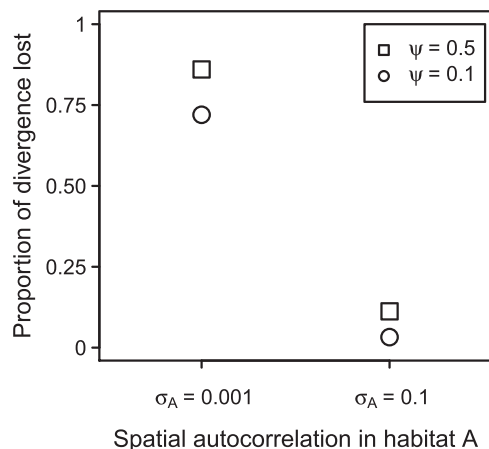
#### DIVERGENCE PERSISTS IN HIGH SPATIAL AUTOCORRELATION LANDSCAPES WITHOUT BEHAVIORAL OR GENETIC LINKAGE BETWEEN LOCI

We find that recombination leads to a near complete loss of divergence in low spatial-autocorrelation landscapes, but has little effect in high spatial-autocorrelation landscapes (Fig. 7). Recombination between the dispersal locus and the ecological specialization locus will only increase gene flow between specialists if both specialists regularly co-occur in space. This can happen when specialists occur in patches with the “wrong” resource type, as discussed above (see section *Competitive exclusion promotes divergence in dispersal strategy when specialization is weak*), or in patches that contain both resource types together (hereafter referred to as “mixed resource” patches). The total number of mixed resource patches in a landscape is independent of the spatial autocorrelation of the resources. We find that, in landscapes with low and moderate spatial autocorrelation, both specialists persist at moderate abundances in mixed resource patches (Fig. 8). However, in high spatial autocorrelation landscapes, specialists on the less auto-correlated





**Figure 6.** Numbers of *A* specialists and *B* specialists after  $2 \times 10^5$  generations in patches of each resource type with and without competition. (A) and (B) show replicates with strong specialization ( $s_a = s_b = 0.50$ ); (C) and (D) show replicates with weak specialization ( $s_a = s_b = 0.05$ ). Note that abundances in (A) and (C) combine cases from unique replicates with *A* specialists alone and *B* specialists alone, while (B) and (D) show abundances of *A* and *B* specialists coexisting on the same landscapes. Results are shown here for the high spatial autocorrelation case ( $\sigma_A = 0.1$ ); see Fig. S5 for the low autocorrelation case. Points represent means across 100 different landscapes; the same 100 landscapes were used for all cases. All parameters except  $s_a$ ,  $s_b$ , and  $\sigma_A$  held the default values shown in Table 1.



**Figure 7.** The effect of recombination on divergence in dispersal probability when ecological specialization is strong ( $s_a = s_b = 0.5$ ). Points indicate the proportion of divergence between habitat types that is lost when recombination increases from  $\psi = 0$  to  $\psi = 0.1$  (circles) or  $\psi = 0.5$  (squares). All parameters but  $\psi$ ,  $s_a$ ,  $s_b$ , and  $\sigma_A$  held the default values shown in Table 1.

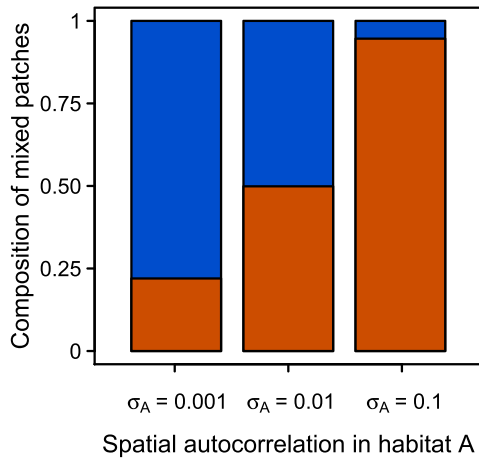
resource are excluded from mixed resource patches, such that 95% of individuals in mixed resource patches are specialists on the high spatial autocorrelation resource (Fig. 8). Therefore, the

effect of random mating and recombination appears to differ in high and low spatial autocorrelation landscapes because competitive exclusion from mixed resource patches reduces opportunities for recombination in highly autocorrelated landscapes.

The reason competitive exclusion is stronger in cases with one highly autocorrelated resource is likely due to propagule pressure. Specialists can dominate mixed resource patches in strongly autocorrelated landscapes even though neither specialist has a local fitness advantage because they have an immigration advantage. Mixed resource patches often appear as small “islands” within larger clusters of the more spatially autocorrelated resource; therefore, they have, on average, more neighboring patches that contain the resource with higher autocorrelation (Fig. S6). Consequently, there are more colonization opportunities for immigrants from that resource type. Furthermore, once dispersal strategies have become locally adapted, individuals adapted to the more autocorrelated resource are more likely to disperse and will, therefore, make up a larger fraction of immigrants across the landscape.

## Discussion

There are several selective forces that typically act on dispersal (for reviews, see Bowler and Benton 2005; Ronce 2007; Duputié



**Figure 8.** The proportion of specialists of each type within habitat patches that contain both resources together. A specialists are in red and B specialists in blue. Both specialists have equal abundance when their “best” habitats do not differ in spatial autocorrelation ( $\sigma_A = 0.01$ ). Points represent means across 100 different landscapes. Local adaptation is strong ( $s_a = s_b = 0.50$ ), but this result does not change appreciably when local adaptation is weak ( $s_a = s_b = 0.05$ ). All parameters but  $s_a$ ,  $s_b$ , and  $\sigma_A$  hold the default values shown in Table 1.

and Massol 2013). Temporal heterogeneity (e.g., disturbance) favors dispersal by giving a short-term fitness advantage to dispersers who arrive shortly after a disturbance has occurred (and thus, the patch is empty or at low density). Temporal heterogeneity also allows bet-hedging that spreads a genotype across multiple patches and reduces the likelihood that all individuals with that genotype will be lost in a single disturbance event (Comins et al. 1980). Dispersal also helps individuals avoid competition with kin, as dispersers compete less with the kin they leave behind (Hamilton and May 1977; Frank 1986; Taylor and Frank 1996). Furthermore, dispersal away from closely related siblings can help individuals avoid inbreeding (and, thus, inbreeding depression; Perrin and Mazalov 1999; Roze and Rousset 2005). On the flip side, dispersal may be selected against if it has direct costs (e.g., requires investment in morphological adaptations, exposes one to higher predation, or requires energy expenditure; but see Fronhofer et al. (2015) for unexpected effects of maternal costs). In spatially heterogeneous environments, dispersal has also been shown to move individuals from higher quality habitat to lower quality habitat more often than the converse, which creates another potential cost to dispersal (Hastings 1983).

Here, we have constructed a model where periodic disturbance and weak kin selection favor the evolution of increased dispersal propensity. Spatial resource heterogeneity in our model creates costs to dispersal by allowing individuals to disperse into lower quality habitat patches. Increasing spatial autocorrelation in resources increases the probability that dispersers will encounter

suitable habitat when dispersing, thus weakening selection against dispersal imposed by the presence of unsuitable patches. The strength of specialization and presence or absence of competitors then influences the strength of selection against dispersing to patches of the “wrong” resource type.

Our primary aim was to understand how the presence of multiple resource types that differ in their spatial autocorrelation influences the evolution of dispersal. We found that whether local adaptation in dispersal strategies arose on resources with different spatial distributions depended on the strength of spatial autocorrelation of those resources: divergence always occurred when at least one resource was highly spatially autocorrelated, but occurred only under a narrow set of conditions when spatial autocorrelation of both resources was low. We chose to explore three discrete levels of spatial autocorrelation in depth to make qualitative predictions about how landscape structure influences the conditions where divergence in dispersal strategy can arise. However, we recognize that exploring a more continuous gradation of spatial autocorrelations could reveal subtler shifts in the exact points where divergence arises, and suggest this as a worthwhile pursuit in the future.

We investigated the consequences of specialization in a second ecological trait not related to an individual’s dispersal strategy. We found that, in general, ecological specialization widened conditions under which dispersal strategies diverged between resource types. In highly autocorrelated landscapes, ecological specialists tended to be spatially restricted to patches of their highest fitness resource under both weak and strong selection. When specialization was strong, this was because high mortality prevented their long-term persistence in patches that did not contain the resource to which they were adapted; when specialization was weak, however, it was competition between different ecological specialists that limited occupancy in patches containing the “wrong” resource type. The resulting differences in habitat use subsequently led to divergent selection on dispersal strategies between specialists. Competition between specialists also affected opportunities for gene flow. When one resource was highly spatially autocorrelated, the specialist on that resource excluded the second specialist from regions of resource overlap so that both specialists rarely co-occurred on the landscape. This reduced mating rates between different specialists and thereby limited opportunities for and consequences of recombination.

Consistent with earlier work, we found that increasing spatial autocorrelation led to an increase in dispersal frequency (Hovestadt et al. 2001; Bonte et al. 2010). This appears to be robust to different model configurations and methods of specifying the shape of the dispersal kernel. Also in line with previous work (Hovestadt et al. 2001), we found that the effect of resource abundance on dispersal propensity was relatively weak. While the focus of our study is to compare between different cases within

our model framework, we can use previous studies to provide coarse theoretical benchmarks to understand how different factors contribute to selection on dispersal within our simulations. In general, evolved rates of dispersal in our model were relatively high compared to the expected evolutionarily stable strategies predicted by either patch disturbance or kin selection alone in spatially heterogeneous landscapes. Using our default parameters for disturbance rate ( $\delta$ ) and resource abundance ( $f$ ), and being relatively liberal with our interpretation, we can use equation (7) in Cheptou and Massol (2009) to determine that disturbance alone should select for an ESS dispersal rate of 0.14. Similarly, we can use our default  $K$  and equation (11) from Taylor and Frank (1996) to find an ESS dispersal rate under kin selection alone of 0.07. In our model, rates of dispersal are consistently higher than these values. Therefore, some additional factors within our model favor increased dispersal rates. Even in landscapes with zero autocorrelation, we find higher values, so our evolved dispersal rates cannot be attributed solely to spatial autocorrelation. Model runs with larger  $K$  do match these predicted ESS values better, suggesting that the high rates of dispersal here might, at least partially, be due our low carrying capacities. Low carrying capacity reduces the size of the local pool of dispersers, causing empty patches to remain below carrying capacity for longer. This could provide an additional benefit to dispersers who reach those patches.

Contrary to our expectations, we found greater divergence evolved in scenarios that favored higher rates of dispersal (Figs. 4, 5,  $\sigma_A = 0.1$ ). This is because the highly autocorrelated landscapes that selected for increased dispersal also allowed for more effective exclusion of competitors: neighboring patches in highly spatially autocorrelated landscapes are rapidly recolonized after local extinction and remain at or near carrying capacity. In contrast, in weakly autocorrelated landscapes, patches were unoccupied for longer after disturbance (Fig. S7) and were typically further below carrying capacity (Fig. S5). This creates more opportunities for colonization by the “wrong” specialist and thus reduces divergent selection on dispersal and increases opportunities for gene flow.

We did not investigate evolution at the ecological specialization locus (e.g., by allowing individuals to evolve to become more or less specialized) in our model. However, even an extremely weak advantage on one habitat led to local competitive exclusion of the alternative specialist and spatial segregation between specialists, indicating that very little variation at this locus is necessary to produce multiple co-existing specialist strategies. We rarely saw extinction of either specialist, regardless of specialization strength, which suggests that coexistence of multiple ecological specialization alleles occurs under a wide range of conditions in our model. We therefore suspect that our general conclusions about local adaptation should hold for extensions that allow evolution to occur in both traits; however, further research

in this area could reveal unexpected interactions when both traits are evolving simultaneously, in particular by allowing for the emergence of generalists and specialists on the same landscape (Nurmi and Parvinen 2011). The opportunity for generalist types on the landscape could prove particularly interesting when considering dynamics in mixed resource patches, as habitat boundaries can serve as refuges for generalists (Débarre and Lenormand 2011).

We find that the combined effects of random mating and recombination differ in landscapes with high versus low spatial autocorrelation. This suggests that selection on factors that create genetic associations between loci, such as recombination or mate choice, should also depend on the strength of spatial autocorrelation in underlying resources. If a population is specialized on a resource that is weakly clustered in space, patches often comprise a mix of locally adapted and maladapted genotypes and, thus, the locally adapted genotypes should benefit from an ability to choose mates of their own kind. This should lead to an overall increase in frequency of an assortatively mating genotype. In contrast, because specialists on highly spatially autocorrelated resources exclude competitors from other resource types, the risk of mating with maladapted individuals is low and, thus, the benefit to being choosy is small.

There are two general areas where we see limitations, and thus, natural extensions to the work we have presented here. The first limitation is in the genetic realism underlying the dispersal kernel. The strength of the method we have used for specifying an individual's dispersal kernel is its flexibility. However, in nature, the shape of species' dispersal kernels likely reflect numerous phenotypic and genetic constraints. Mutation in our model, which redistributes probability between two bins at a time, is not genetically realistic. Furthermore, this method has some bias toward producing more uniform mutant kernels, which may slow the speed of evolution by reducing variation in segregating kernel types. Consequently, our approach, which does not account for such constraints, may not be useful for exploring processes such as short-term responses to environmental perturbation or the speed of adaptation, both of which should be sensitive to genetic architecture (Saastamoinen et al. 2018). The inclusion of diploidy and dominance effects has also been shown to allow for the persistence of dispersal polymorphisms in single-resource landscapes, and has the potential to alter the effects of assortative mating by dispersal phenotype (Fronhofer et al. 2011). Therefore, future work could evaluate the robustness of our conclusions to different genetic architectures.

The second area where we anticipate ready extensions of this model is in the structure of the landscape. We have used a landscape formulation that provides a reasonable approximation for discrete resource types (e.g., presence or absence of two host plants for plant-feeding insects); however, this approach

is not entirely appropriate for resources that vary in abundance continuously across space. Such resources could, for example, lead to higher rates of gene flow and, therefore, less divergence. A next logical step would be to construct landscapes that vary continuously in *abundance* rather than simply *presence*. In nature, different habitat types can also be correlated or anti-correlated in space, and examining how the correlation between habitat types influences competition and divergence could also prove fruitful. Spatial autocorrelation in which patches experience local extinction can also influence the evolved rate and distance of dispersal (Fronhofer et al. 2014), as could altering the intensity of disturbance events.

Our results indicate that, in systems with two discrete resource types, differences in the spatial distribution of resources can produce close to complete spatial segregation of alleles conferring any local advantage. The strength of specialization determines whether this spatial separation is due to the direct effects of mortality or, instead, competitive displacement by a weakly superior specialist. Assortment by resource type creates opportunities for selection to act separately on populations carrying one or the other specialist allele, which then generates local adaptation in dispersal strategies of populations occupying each resource type. We have shown that, in multi-resource landscapes, the evolutionary trajectories of dispersal-related traits depends fundamentally on both the spatial structure of those resources and the selective processes that operate within each of them.

#### AUTHOR CONTRIBUTIONS

M.C. conceived the initial idea for the study. M.C. and L.M. both designed and built the model and drafted the manuscript. Both authors gave final approval for publication.

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#### DATA ARCHIVING

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## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** Population mean probability of leaving the natal patch after  $2 \times 10^5$  generations, beginning with different starting dispersal kernels.

**Figure S2.** Population mean probability of leaving the natal patch after  $4 \times 10^5$  generations with higher patch carrying capacity ( $K = 100$  instead of  $K = 10$  as in the main text).

**Figure S3.** Population mean probability of leaving the natal patch after  $2 \times 10^5$  generations with 10 or 100 strategies segregating in the population at time.

**Figure S4.** Population mean probability of leaving the natal patch in landscapes with weak ecological specialization ( $s_a = s_b = 0.05$ ).

**Figure S5.** Total numbers of *A* specialists and *B* specialists after  $2 \times 10^5$  generations in each patches of each resource type with and without competition.

**Figure S6.** Number of edges between mixed resource patches and resource *A* (red), resource *B* (blue) and other mixed resource patches (purple).

**Figure S7.** Patches containing both resources or highly autocorrelated resource types are re-colonized fastest.