

Co-evolution of dormancy and dispersal in spatially autocorrelated landscapes

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The evolution of dispersal can be driven by spatial processes, such as landscape structure, and temporal processes, such as disturbance. Dormancy, or dispersal in time, is generally thought to evolve in response to temporal processes. In spite of broad empirical and theoretical evidence of trade-offs between dispersal and dormancy, we lack evidence that spatial structure can drive the evolution of dormancy. Here, we develop a simulation-based model of the joint evolution of dispersal and dormancy in spatially heterogeneous landscapes. We show that dormancy and dispersal are each favored under different landscape conditions, but not simultaneously under any of the conditions we tested. We further show that, when dispersal distances are short, dormancy can evolve directly in response to landscape structure. In this case, selection is primarily driven by benefits associated with avoiding kin competition. Our results are similar in both highly simplified and realistically complex landscapes.

KEY WORDS: Diapause, kin selection, movement, migration, quiescence, spatial clustering.

Dormancy and dispersal have long been considered alternative strategies for dealing with environmental uncertainty (Buoro & Carlson, 2014; Venable & Brown, 1988). Dispersal allows parents to spread their offspring through space, which reduces the risk that all offspring will suffer from the same local disasters (Blanquart et al., 2013; Comins et al., 1980; Fronhofer et al., 2014; Levin et al., 1984) while dormancy, which is sometimes referred to as “dispersal in time” (Buoro & Carlson, 2014; Venable & Brown, 1988), allows parents to spread their offspring across years, reducing the risk that all offspring will die in a bad year (Buoro & Carlson, 2014; McPeck & Kalisz, 1998; Mathias & Kisdi, 2002; Philippi & Seger, 1989; Rajon et al., 2009). These two mechanisms for avoiding disturbance have long been thought to be largely redundant, and empirical and theoretical studies have sometimes found trade-offs between them (Chen et al., 2020). However, few theoretical studies have allowed dispersal and dormancy to evolve simultaneously, making inferences about trade-offs difficult to confirm (but see Klinkhamer et al., 1987; McPeck and Kalisz, 1998; Vitalis et al., 2013).

In addition to help some offspring avoid locally unfavorable conditions (a process known as bet-hedging), dispersal can

evolve via kin selection because it can reduce local competition between relatives (Bonte et al., 2010; Hamilton & May, 1977; Hovestadt et al., 2001). Dormancy, like dispersal, has the potential to reduce kin competition by separating kin through time (Kobayashi & Yamamura, 2000). The effectiveness of dormancy for moderating kin competition should, hypothetically, depend on the level of dispersal, as both processes decrease the relatedness of local competitors (Kobayashi & Yamamura, 2000). However, explicit consideration of the effects of kin competition in work that examines evolution of both dormancy and dispersal evolution are rare (to our knowledge, only Vitalis et al., 2013). This may be due to the intractability of density-dependence in analytical models of dormancy and dispersal. Kin competition only occurs if population regulation is density-dependent; without density-dependence, an individual does not benefit when their neighboring kin disperse away or go dormant. In analytical models of dispersal and dormancy, density-dependence is difficult to implement and, consequently, growth is often assumed to be density-independent (Klinkhamer et al., 1987; McPeck and Kalisz, 1998; Venable & Brown, 1988). Here, we incorporate density-dependence by using an

individual-based simulation framework that does not suffer these analytical difficulties.

Dispersal evolution is impacted not only by variation in habitat quality through time but also by variation in habitat quality through space (Gadgil, 1971; Hovestadt et al., 2001; Snyder, 2011). When resources are highly clustered in space, local dispersal often moves an individual between locations of similar quality and, consequently, the strong benefits of dispersal that result from kin competition ultimately favor high rates of dispersal (Bonte et al., 2010). In contrast, when resources are more fragmented, local dispersal is risky because it often moves an individual into a low quality habitat and, thus, lower rates of dispersal are optimal (Hastings, 1983). Because dormancy is a temporal process, it is generally assumed to arise because of temporal resource variation (Wilsterman et al., 2021), which has been the focus of previous research (Rajon et al., 2009; Snyder, 2006). While effects of spatial habitat autocorrelation on dispersal have been identified (Cenzer & M'Gonigle, 2019; Hovestadt et al., 2001), and dispersal and dormancy have both been shown to influence one other (Kobayashi & Yamamura, 2000; Mathias & Kisdi, 2002; Vitalis et al., 2013), the potential impact of spatial autocorrelation on dormancy remains largely unexplored. In part, this may be due to the analytical challenges of modeling spatially complex landscapes versus simple landscapes that comprise discrete patches. While discrete patch landscapes might be appropriate representations of some systems (e.g., islands), many organisms experience the landscape as a more complex gradient of higher and lower quality habitats. Furthermore, discrete patch models necessitate specific assumptions about dispersal costs, patch connectivity, and within patch dynamics, that can complicate dynamics and interpretation.

Here, we hypothesize that spatial autocorrelation in resources may impact dormancy evolution either directly or indirectly via selection on dispersal. We evaluate this first using a simple landscape structure and then expand to more complex landscapes.

Model Description

We construct an individual-based model where asexual individuals compete locally for resources across a spatially continuous two-dimensional landscape. These resources are necessary for reproduction, with stronger experienced competition reducing fecundity. Individuals are characterized by two evolving quantitative traits that determine dormancy probability and dispersal distance, respectively. Every generation, each individual, dormant or not, experiences stochastic mortality. Survivors then either enter dormancy (which lasts for a single generation), or mature and join those that are emerging from dormancy to create the next genera-

tion of reproductive adults. Before competition and reproduction, individuals disperse away from their natal locations. Finally, non-dormant individuals compete for resources locally before reproducing and finally dying. In further sections, we describe each model step in more detail. Parameter and variable definitions are provided in Table S1.

LANDSCAPES

We situate our model runs in static resource landscapes where resources are distributed across space with a specified degree of spatial heterogeneity. We let $k(x, y)$ denote the amount of resource available at location (x, y) for x and y each in $[0, 1)$. We normalize the landscape, so that the total amount of resources, $\iint k(x, y) dx dy$, is equal to 1. All boundaries are wrap-around to avoid edge effects.

For the majority of the results we present in the main text, we use simple landscapes defined by a specified number, n_p , of “patches” (see Table S1) of equally-sized high quality habitat separated by patches of equally-sized low quality habitat (Figure 1A), so that each habitat type makes up half the landscape and each patch has width $\frac{1}{2n_p}$. We assume that low quality habitat contains half the quantity of available resources as high quality habitat ($k(x, y) = \frac{2}{3}$ and $\frac{4}{3}$, respectively). We compare these to homogeneous landscapes, where all locations have equal resources ($k(x, y) = 1$).

Later, we extend our findings from these simple landscapes to more realistic spatially autocorrelated landscapes. To generate these landscapes, we follow the methods described in Haller et al. (2013), where our *acl* corresponds to their parameter l_g (and other parameters were $s = 0$, $c = 0$, and $a = 1$; see Haller et al. (2013) for details). Higher levels of *acl* correspond to landscapes with resources that are more strongly clustered in space, while lower levels of *acl* correspond to more heterogeneous landscapes (Figure 4A; see *acl* in Table S1 for tested values). Unlike for our simple landscapes, each replicate run here uses a different randomly generated and unique landscape.

POPULATION INITIALIZATION

In each replicate simulation, we initialize model runs by distributing N monomorphic individuals randomly across space. We let (x_i, y_i) , $x_i, y_i \in [0, 1)$ denote the location of individual i and $t_{1,i}$ and $t_{2,i}$ denote their trait values at two quantitative traits that govern dormancy probability and dispersal distance, respectively. For results presented in the study, simulations were initiated with no dormancy ($t_{1,i} = 0$ for all i) and—where dispersal was free to evolve—with $t_{2,i} = 0.05$ for all i . For runs where dispersal was not free to evolve, we considered $t_{2,i} = 0.01, 0.05$, or 0.50 , for all i . For runs where dormancy was not free to evolve, we considered $t_{1,i} = 0.10, 0.30$, or 0.50 for all i .

MORTALITY

Each generation, individuals have a probability d of dying before reaching reproductive maturity. Individuals who enter dormancy are subjected to this random mortality twice (once in each time step).

DORMANCY

Individuals either mature immediately or enter dormancy, thereby delaying maturation for a single generation. For individual i , the latter outcome occurs with probability $t_{1,i}$ (their trait value at the first quantitative trait). We do not consider dormancy that lasts for multiple generations.

DISPERSAL

Before maturation, individuals who did not enter dormancy, along with those newly emerged after dormancy, disperse from their natal locations with dispersal kernels dictated by their trait values at trait t_2 . Specifically, individual i disperses a distance that is drawn from a Gaussian function centered at zero with standard deviation $t_{2,i}$. Movements occur in all directions with equal probability and landscape boundaries are wrap-around.

In some scenarios, we consider populations that are monomorphic at their dispersal traits (and also not evolving). In those cases, we use σ_m to denote the width of the Gaussian dispersal kernel that characterizes dispersal for all individuals.

COMPETITION FOR RESOURCES

The competitive impact of individual j on individual i , which we denote by ψ_{ij} , decreases with increasing distance between them, d_{ij} , according to a Gaussian function with standard deviation σ_s . Specifically,

$$\psi_{ij} = \frac{\exp(-d_{ij}^2/2\sigma_s^2)}{2\pi\sigma_s^2}. \quad (1)$$

Through competition, individual i is able to acquire ρ_i resources, where

$$\rho_i = \frac{k(x_i, y_i)}{\sum_j \psi_{ij}}, \quad (2)$$

where x_i and y_i denote individual i 's x and y -coordinates, and the sum is taken over all individuals. Given the above, an individual acquires more resources when they are in a location with high resource abundance (large $k(x_i, y_i)$) and/or if they have few nearby competitors (small $\sum_j \psi_{ij}$).

REPRODUCTION

Individuals reproduce asexually. An individual's expected reproductive success is higher if it has acquired a greater total amount

of resource. Specifically, we calculate the fecundity of individual i as

$$f_i = \tau_i \cdot f_{\max}, \quad (3)$$

where

$$\tau_i = \frac{\rho_i}{c + \rho_i} \quad (4)$$

denotes an individual's competitive fitness, f_{\max} is the maximum possible expected fecundity, and c determines how quickly competitive fitness increases with acquired resource amount, ρ_i . When $\rho_i = c$, for example, $f_i = 1/2 \cdot f_{\max}$, and an individual obtains half of the maximum possible fecundity. When $c = 0$, all individuals have the same expected fecundity, regardless of differences in acquired resource amounts. In general, as c increases, differences in competitive fitness resulting from differences in acquired resource amounts become greater and, therefore, we refer to c as the "strength of competition for resources." Note, however, that this is not necessarily always the case for the functional form in Equation 4 (see M'Gonigle & Greenspoon, 2014, for additional details). Individual i 's realized fecundity is drawn from a Poisson distribution with mean f_i . Offspring inherit parental trait values and, for scenarios where traits evolve, with added mutational effects which are drawn from a Gaussian distribution centered at zero and with standard deviation σ_μ (and the added constraints that values of $t_{1,i}$ are constrained to the interval [0,1] and values of $t_{2,i}$ are constrained to be non-negative). After reproduction parents die.

KIN COMPETITION

In our model, "relatedness" is equivalent to phenotypic similarity; thus, kin selection acts when an individual increases or decreases the fitness of another individual who is more phenotypically similar to them than average. For dormancy, we can directly calculate the impact of kin competition by evaluating how much local competition is reduced by one's neighbors going dormant. If neighbors are closely related, that is, phenotypically similar, then dormancy will disproportionately reduce competition for individuals with high dormancy trait values ($t_{1,i}$). To calculate this benefit, we first calculated the competitive fitness, τ_i (see Equation 4) for all active (non-dormant) individuals on the landscape at the final time point of each model run. We then re-calculated this quantity treating all dormant individuals as if they were participating in competition. The difference between these two values is a measure of the benefit to an individual from its neighbors going dormant that we here call the change in competition ($\Delta\tau$) from dormancy.

Results

We find that when patches are large (patch width > 0.05 , $n_p = 1 - 10$), increasing patch size leads to longer dispersal distances (larger $t_{2,i}$ values), consistent with earlier work (Cenzer & M'Gonigle, 2019; Hovestadt et al., 2001), as individuals dispersing from larger patches are more likely to land in high quality habitat (Figure 1B). However, below a threshold patch size (here, patch width < 0.045 , $n_p > 11$), we see the opposite pattern, with appreciably longer dispersal distances as patches become smaller (Figure 1B). In these highly heterogeneous landscapes, patches are so small that even very local dispersal is reasonably likely to move an individual beyond the edge of its origin patch and into low quality habitat. Thus, both long and short dispersal distances entail similar risks. However, greater dispersal distances further reduce kin competition and, thus, selection favors increasingly global dispersal. When patches are sufficiently small (patch width = 0.016), dispersal distance evolves to a level equivalent to homogeneous landscapes (“H” in Figure 1B).

We find that dormancy co-evolves with dispersal across landscape types (Figure 1C). As patch size decreases and dispersal evolves to become more local, evolution favors increasing dormancy probability as a temporal, rather than spatial, means to avoid kin competition. We find that dormancy probability declines again once patch sizes fall below a threshold (patch width < 0.045), mirroring the increases in dispersal documented above (Figure 1C). Thus, as dispersal increases, dormancy decreases, and vice versa, with dormancy favored at moderate spatial heterogeneities and dispersal favored at both extremes.

Next, we look more closely at how dispersal and dormancy evolve in each individual replicate simulation (Figure 1D). Here, we find a strong negative correlation between dispersal and dormancy, with no case evolving high or intermediate levels of both. This is particularly striking in the range that comprise the “threshold” at which evolution transitions from favoring dispersal to favoring dormancy (patch width = 0.033 – 0.045). In this region, mean dispersal and mean dormancy (means are calculated across replicate simulation runs) are both intermediate (Figure 1B,C). However, individual runs either evolve high dispersal or high dormancy, but never both (Figure 1D). This indicates 1) that there is a strong trade-off between dormancy and dispersal and 2) that whether evolution favors dormancy or dispersal can depend on which mutations happen to arise and fix first.

To confirm that kin competition is, indeed, the process favoring dormancy, we show that, on average, individuals with higher dormancy probabilities (larger $t_{1,i}$) gain a greater benefit from dormant neighbors than individuals with lower dormancy probabilities (Figure 2). If neighbors are more closely related and, therefore, more phenotypically similar, individuals with higher dormancy probabilities should gain a greater benefit from their

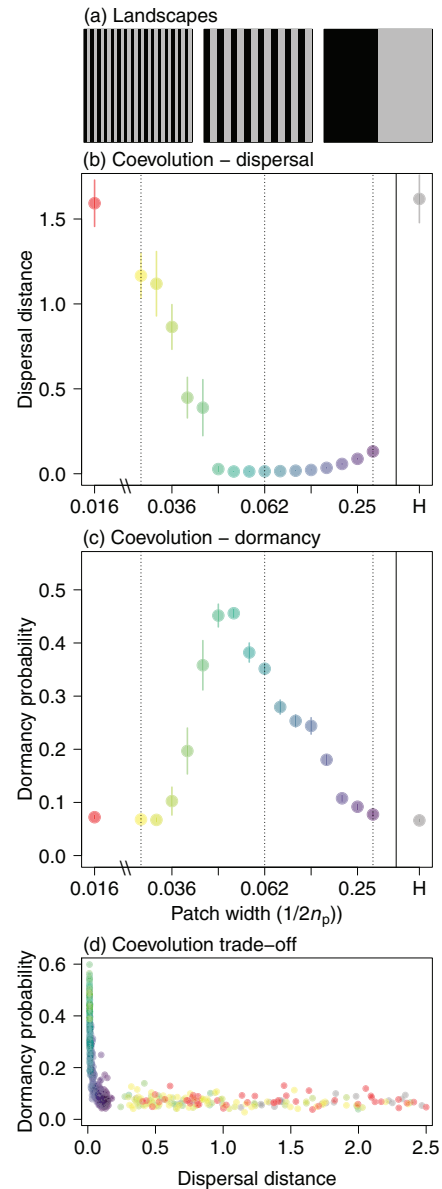


Figure 1. Co-evolution of dormancy and dispersal on simplified landscapes. (A) Landscapes with $n_p = 16, 8,$ and 1 , corresponding to patch widths of $1/2n_p = 0.031, 0.062,$ and 0.5 . (B) Evolved dispersal distances and (C) dormancy probabilities on landscapes with patch widths from 0.031 to 0.5 (yellow to purple) and 0.016 (red). Grey points represent evolved dormancy and dispersal on homogeneous landscapes. Points and vertical bars are means and standard errors across 30 replicate model runs. Dotted vertical lines correspond to the 16, 8, and 1 patch landscapes shown in panel (A). (D) The trade-off between dormancy probability and dispersal distance across simulations. Colors correspond to landscape values as in (B) and (C); each point represents the mean evolved dispersal distance and dormancy probability for a single model run after 10^5 generations. Note that, for an intermediate number of patches (greens), the same conditions can yield points at either the upper left or lower right. The x-axis was truncated (excluding points with dispersal distances between 2.5–4.5) to better enable visualization of clustered points along the y-axis.

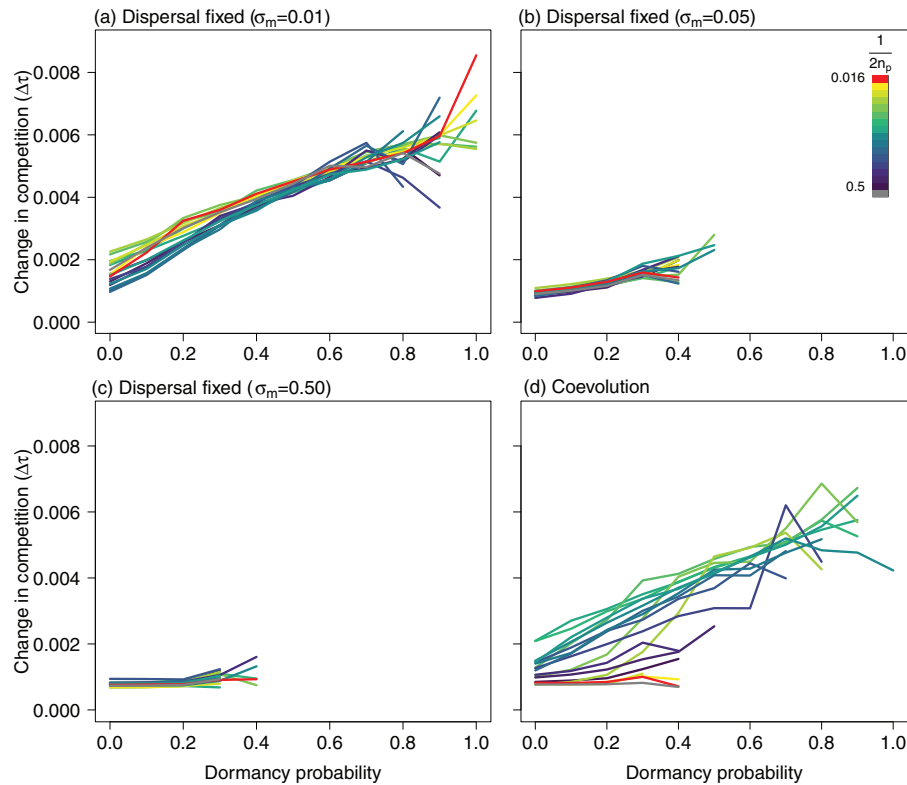


Figure 2. Change in the strength of competition with and without dormancy. In panels (A–C), dispersal probability was fixed and not evolving, whereas dormancy probability was free to evolve and, thus, differed between individuals. In panel (D), both dispersal probability and dormancy probability were free to evolve. Each line shows the average relationship between an individual's dormancy probability and the benefit that individual receives from others nearby going dormant. When dispersal is low (A), increasing dormancy correlates with reduced competition from kin. When dispersal is moderate (B) or high (C), dormancy typically remains low and there is little reduction in kin competition from dormancy. When dispersal is free to evolve (D), moderate levels of landscape heterogeneity generate a positive relationship between dormancy and reduced kin competition.

neighbors becoming dormant. Indeed, we find that when dispersal is low and, thus, kin more spatially clustered, individuals with larger $t_{1,i}$ trait values gain greater competitive benefits from others becoming dormant (Figure 2A). As rates of dispersal increase, kin become less clustered in space and, consequently, benefits of dormancy on kin decline (Figure 2B, C). When both dispersal and dormancy co-evolve, we can see that benefits resulting from dormancy of neighbors increase and then decrease again as patches become smaller (an inverse pattern than is exhibited for dispersal, Figure 2D). In sum, when higher dispersal evolves, dormancy becomes less valuable for avoiding kin competition, as neighbors are less related and, thus, less phenotypically similar.

We find that the impact of landscape structure on dispersal evolution is moderated by dormancy when dormancy probability is fixed (Figure 3A). When dormancy is fixed at a low level ($q_f = 0.1$), dispersal evolution follows a similar pattern to the co-evolution case: when patches are very small, dispersal distances are long and decrease until reaching an inflection point at patch width = 0.045 (Figure 3A, circles). As patch width increases above 0.045, dispersal distance increases slowly to low but ap-

preciable levels. Fixing dormancy at moderate ($q_f = 0.3$) or high ($q_f = 0.5$) levels shifts this inflection point toward smaller patch sizes (patch width < 0.033 or 0.031, respectively). Thus, when dormancy probability is moderate or high, kin competition is not strong enough to favor dispersal in this range of patch sizes (effectively, populations are held on the left-hand side of the trade-off in Figure 1D). Even at very high landscape heterogeneities (patch width = 0.016), fixing dormancy at moderate or high levels still leads to evolution of shorter dispersal distances than when dormancy is low (Figure 3A, red points). Notably, the impact of fixed dormancy on dispersal seems to disappear when resource availability on the landscape is fully homogeneous (Figure 3A, points “H”).

Interestingly, we find that when dispersal is held constant, dormancy still evolves in response to landscape structure (Figure 3B). First, when dispersal is high ($\sigma_m = 0.50$), there are virtually no benefits of dormancy via reduced kin competition (Figure 2C). Therefore, dormancy evolves to a low level that does not depend notably on landscape structure (Figure 3B, diamonds). When dispersal is fixed at an intermediate-low

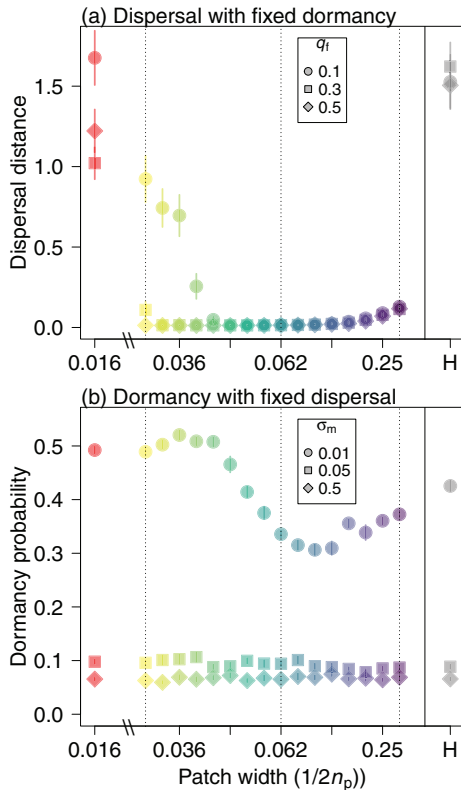


Figure 3. (A) Evolved dispersal distances when dormancy probability is fixed ($t_{1,i} = q_f$ for all i). Dormancy probability moderates the impact of patch width ($1/2n_p$) on dispersal, with higher dormancy probabilities dampening dispersal distance when patches are small. (B) Evolved dormancy probabilities when dispersal distance is fixed ($t_{2,i} = \sigma_m$ for all i). Patch width directly impacts dormancy probability when dispersal distances are short. Points and vertical bars are means and standard errors across 30 replicate model runs after 10^5 generations. See Figure S1 for the similar patterns in noisy landscapes.

level ($\sigma_m = 0.05$), kin competition modestly favors dormancy (Figure 2B). Here, we see dormancy probability evolves to a slightly higher level than for high dispersal; however, any landscape effects are slight (Figure 3B, squares). When dispersal is local ($\sigma_m = 0.01$), individuals rarely escape kin competition by dispersing, and evolution strongly favors high values of dormancy overall (Figure 2A). Here, the optimal dormancy probability is strongly dependent on the landscape structure (Figure 3B, circles). At very small patch sizes (patch width < 0.041 , $n_p > 12$), landscapes are effectively uniform from the perspective of competition; neighboring patches are no longer isolated because competition now spans multiple patches (i.e., the width of competition, σ_s , is large enough relative to the spaces between patches that individuals exert meaningful competitive effects across multiple patches). As patch size increases, dormancy probability declines to an inflection point ($n_p \sim 6$). We hypothesize that this decrease at moderate patch widths is

the result of larger patches increasingly supporting multiple kin groups and, thus, non-relatives can increasingly benefit from kin groups with high dormancy. When patches are large (patch width > 0.083 , $n_p \leq 5$), increasing patch size results in a modest increase in optimal dormancy probability.

Finally, we extend these results to more spatially realistic, “noisy” landscapes with varying degrees of spatial autocorrelation. We find that the co-evolution of dispersal and dormancy show nearly identical results to those for our simple striped landscapes (Figure 4B,C), both in mean evolved levels of dormancy and dispersal across simulations and in the existence of an intermediate “threshold” heterogeneity in which each replicate either evolves high dormancy or high dispersal, but not both (Figure 4D). When dormancy is fixed, we again find that higher rates of dormancy favor the evolution of shorter dispersal distances overall and raise the inflection point in landscape heterogeneity at which long-distance dispersal is favored (Figure S1A). Similarly, when dispersal is fixed, we find the same strong impact of landscape structure on dormancy, but only when dispersal is local (Figure S1B; $\sigma_m = 0.01$).

Discussion

We have shown that static landscape structure impacts dormancy evolution, both indirectly via evolution of dispersal traits and directly via kin selection. By allowing dispersal and dormancy to co-evolve, we confirm the existence of an emergent trade-off between these two mechanisms of kin competition avoidance. We show that the form of this trade-off is dependent on landscape structure, and, in particular, that for some landscapes heterogeneities, either dispersal or dormancy can become the dominant mechanism, but which one “wins” can depend on chance. We further show that these patterns are repeatable as a function of landscape structure emerging in both our simple and more spatially complex landscapes.

Our finding that dispersal and dormancy co-evolve under kin competition is consistent with previous work showing that both dispersal (Cenzer & M’Gonigle, 2019; Hovestadt et al., 2001) and dormancy (Kobayashi & Yamamura, 2000) can evolve via kin competition. We note that while allowing both to co-evolve has often been cited as an area needing further work (Buoro & Carlson, 2014; Snyder, 2006; Venable & Brown, 1988), examples remain rare. The dependence of the co-evolutionary outcome on the landscape likely relates to the changing cost of dispersal in different landscapes. While the direct cost of dormancy in our model is always the same (two rounds of stochastic mortality compared to one), the cost of dispersal depends on patch size. While the cost of dispersal is difficult to quantify numerically in our model, our findings seem to agree with Vitalis et al. (2013) who show that in a discrete-patch model with kin competition

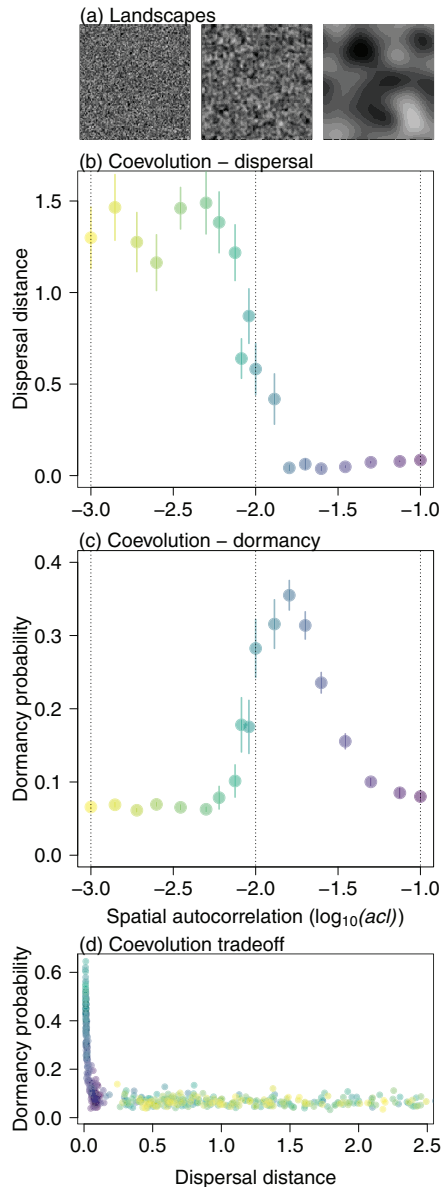


Figure 4. Co-evolution of dormancy and dispersal on randomly generated noisy landscapes. (A) Example landscapes for low, moderate, and high levels of spatial autocorrelation ($acl = 0.001, 0.01,$ and 0.1 , corresponding to $\log_{10}(acl) = -3, -2,$ and -1 on the x-axis, from left to right). (B) Evolved dispersal distances and (C) dormancy probabilities on landscapes with varying levels of spatial heterogeneity. Points and vertical bars are means and standard errors across 30 replicate model runs, each on a unique landscape. Vertical lines in panels B and C denote autocorrelation values used to simulate sample landscapes shown in (A). (D) The trade-off between dormancy probability and dispersal distance across model runs in noisy landscapes. Colors represent the spatial autocorrelation in noisy landscapes; each point represents the mean evolved dispersal distance and dormancy probability for a single model run after 10^5 generations. Note that, for intermediate spatial autocorrelation values (blue-greens), the same conditions can yield points at either the upper left or lower right.

and conditional dispersal, dormancy evolves only when the associated costs are lower than the costs associated with dispersal. Here, we chose a conservatively high cost of dormancy; we expect that relaxing this cost would expand the conditions under which dormancy evolves, and should be explored in future work.

Trade-offs have been demonstrated in models looking at the evolution of dispersal or dormancy. Previous work that sequentially fixed the level of dormancy or dispersal found that when dispersal is lower, dormancy evolves to a higher level, and vice versa (Klinkhamer et al., 1987; Vitalis et al., 2013). We were surprised to find a narrow range of landscape types where either dormancy or dispersal could evolve, but which one dominated seemed to be the result of chance. We posit that this may be similar to the bistable equilibria briefly mentioned in Vitalis et al. (2013) or the saddle point in McPeck and Kalisz (1998). Both sets of authors found that under a narrow range of parameters in discrete patch models, bistable equilibria existed where either dispersal or dormancy could fix, depending on initial conditions. McPeck and Kalisz (1998), whose model included fluctuating fitness via stochastic patch extinction also found that as patch number increases, dispersal was favored over dormancy because the likelihood that all patches simultaneously experience extinction events was low and, thus, dormancy had little benefit, whereas dispersive types were able to recolonize faster. While we have no such analog to stochastic extinction here, we do find that more small patches favors dispersal over dormancy.

Dormancy is typically proposed as a mechanism a parent can use to spread emergence of their offspring over multiple time steps as a way to mitigate the negative impacts of bad years. Perhaps most interesting here, however, is our finding that dormancy can evolve directly as a response to a fixed landscape structure, even in the absence of dispersal evolution. This follows from the fact that different landscape structures directly impact the strength of kin competition that subsequently impacts dormancy evolution. We posit that smaller patch sizes may increase the strength of kin competition by increasing within-patch relatedness. Previous work has shown that decreasing population size can increase kin selection for dormancy, because each dormant individual has a stronger impact on competition when populations are small (Vitalis et al., 2013) and smaller, more isolated patches will have higher relatedness (Kobayashi & Yamamura, 2000).

Our model has limitations and, thus, areas where future exploration may provide additional insights. For example, in our asexual model, “kin” are simply phenotypically similar individuals. Thus, we cannot rule out the possibility that what we call “kin competition” could be spatial clustering of unrelated individuals who independently evolved similar dormancy trait values, although we consider it unlikely. Future work that examines

alternative modes of reproduction and explicitly tracks relatedness could prove fruitful. In addition, we only consider a simple case of passive dispersal, as might characterize many plants, wind-dispersed insects, and marine invertebrates. Considering the impact of landscape structure on organisms with directed dispersal, who may avoid settling in low-quality habitat, but at a higher cost to dispersal, would be an interesting expansion to this work. Finally, while we demonstrate here that landscape structure alone can impact co-evolution between dormancy and dispersal, there is no doubt that temporal heterogeneity is an important contributor to the evolution of both processes in nature. Thus, it would be worthwhile to include both spatial and temporal variation in future work.

We show that landscape structure dictates the outcome of co-evolution of dormancy and dispersal in a way that is remarkably consistent across simplified and complex landscapes. We suggest that considering landscape structure in future studies of dormancy evolution, as well as dormancy-dispersal co-evolution, would be fruitful. While dormancy has traditionally been viewed primarily as a means to adapt to temporal processes, we suggest here that both empirical and theoretical studies of dormancy would benefit from considering purely spatial selection pressures as well.

AUTHOR CONTRIBUTIONS

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

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

Data is publicly archived on Dryad at: <https://doi.org/10.5061/dryad.dbrv15f40>

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Supporting Information

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

Table S1: Model parameters and model variables.

Table S2: Summary of modelled features in relevant theoretical papers.

Figure S1: (A) Evolved dormancy probabilities on noisy landscapes when dispersal distance is fixed at low ($\sigma_m = 0.01$, circles), moderate-low ($\sigma_m = 0.05$, squares), and moderate-high ($\sigma_m = 0.5$, diamonds) values.