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Short title: Evolution and population spread

The influence of evolution on population spread through patchy landscapes

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ABSTRACT

Predicting the spatial advance of biological invasions and range-shifting native species under climate change requires understanding how evolutionary processes influence the velocity of spread. Although landscape heterogeneity and the finite nature of individuals are known to influence the ecological dynamics of spreading populations, their effect on evolutionary dynamics influencing spread is poorly understood. We used adaptive dynamics and simulation approaches to evaluate the direction of selection on demographic and competitive traits in annual plant populations spreading through linear landscapes. In contrast to models in homogeneous environments where low-density fecundity is selectively favored, we found that large gaps between suitable habitat could favor the rise of competitively tolerant individuals at the invasion front, even when this ability to tolerate competitors came at the cost of reduced fecundity when rare. Simulations of the same processes incorporating finite individuals revealed a spatial priority effect; the long-term outcome of evolution strongly depended on which strategy initially got ahead. Finally, we found that although evolutionary change in demographic and competitive traits could increase the spread velocity, this increase could be insignificant in patchy landscapes, where competitive traits were favored in both spreading and non-spreading populations.

INTRODUCTION

How populations spread across landscapes underlies two pressing ecological concerns: biological invasions (Williamson 1996; Pyšek and Hulme 2005) and range shifts induced by climate change (Parmesan and Yohe 2003; Root et al. 2003). Introduced species are only invasive if they spread in their new range, and native species can only expand their ranges to track warming climate by spreading to new locations. While the ecological controls over the spread process have been subject to extensive research (Skellam 1951; Okubo and Levin 2001; Hastings et al. 2005), the role of evolutionary processes in regulating population expansion has, until recently, received little attention (Travis and Dytham 2002; Holt et al. 2005; Phillips et al. 2010; Perkins et al. 2013).

Much of our current understanding of how evolution influences spread builds on theoretical models of population dynamics in continuous landscapes. One lesson from these models is that individuals at the front of the invasion, growing at low density, contribute the offspring that advance the population forward (Kot et al. 1996; Levin et al. 2003; Hastings et al. 2005). As a consequence, the spread process itself and the spatial sorting that results (Shine et al. 2011) often impose strong selection for greater dispersal and greater low-density versus high-density reproduction (Travis and Dytham 2002; Holt et al. 2005; Burton et al. 2010; Perkins et al. 2013). Although dispersal and low-density reproduction, the two traits that determine invasion velocity in continuous landscapes (Lewis and Kareiva 1993; Wang et al. 2002), may trade off with those determining competitive tolerance, or the ability of individuals to maintain reproductive output at high density (reviewed in Burton et al. 2010), individuals in the rear of the invasion contribute little to expansion in most spread models for continuous landscapes.

Assuming no swamping effects of gene flow (Holt et al. 2005), rapid evolution of dispersal and

demographic rates at the invasion front can increase the speed of the invasion (Travis and Dytham 2002; Phillips et al. 2008; Burton et al. 2010; Perkins et al. 2013). This contrasts with models without evolution, which predict constant invasion velocities under most conditions (but see e.g. Kot et al. 2004).

Two simplifications in these mathematical and simulation models limit their applicability to natural settings. The first is the assumption that the landscape is homogeneously favorable. Both cellular automata and analytical approaches have relaxed this assumption and support the intuitive expectation that the inclusion of unfavorable habitat slows the spread velocity (With and Crist 1995; Higgins et al. 2003; Kawasaki and Shigesada 2007; Dewhirst and Lutscher 2009; Engler and Guisan 2009; Travis et al. 2010; Phillips 2012; Boeye et al. 2013; Henry et al. 2013; Gilbert et al. 2014). Recent work has further shown that the inclusion of unfavorable habitats can change the fundamental way invasions progress (Pachepsky and Levine 2011). In landscapes where gaps between suitable habitat are sufficiently large, leading individuals are rarely at low density, because populations tend to build up behind the gap, and only occasionally advance. This build-up leads to a strong influence of density dependence on the invasion speed in patchy landscapes (Pachepsky and Levine 2011). This result presumes that populations contain discrete numbers of individuals; otherwise some infinitesimally small amount of seed reaches all patches in the entire landscape (Mollison 1991; Clark et al. 2001).

This requirement for discrete individuals in the population raises the second limitation of mathematical and simulation models of evolution during population spread—the common assumption of continuously varying population densities. Recent work suggests that when models incorporate the finite nature of individuals in spreading and evolving populations, genetic drift rather than natural selection can determine the genotypes at the invasion front (Klopfenstein et

al. 2006; Excoffier et al. 2009). However, the majority of theoretical studies thus far have tended to examine traits that have little potential to influence the spread velocity (Excoffier and Ray 2008), and thus the link between the finite nature of individuals in evolving populations and the extent to which evolution can influence spread is only beginning to be explored. Given that biological invasions often begin with only a few introduced individuals (before sometimes growing to large sizes), stochastic events early in the spread process may have lasting impacts on the dynamics of some expanding populations.

In sum, although models consistently suggest that evolution differs at the front versus the back of invasions, how landscape patchiness and the discreteness of individuals influence how evolution changes the invasion velocity is poorly understood. In this paper, we address the following three questions: 1) How does landscape patchiness change the selective environment for demographic and competitive traits in spreading populations? 2) How does the finite nature of individuals in spreading populations influence the optimal strategy? 3) How does landscape patchiness influence the degree to which evolution can influence the spread velocity? We expected selection on demographic traits to differ in continuous versus patchy landscapes because the relative influence of demographic traits controlling invasion speed—low-density fecundity and competitive tolerance—changes when landscapes contain large gaps between suitable habitat (Pachepsky and Levine 2011). Moreover, if these traits trade off against one another, landscape patchiness should have great potential to affect the selective environment and impact the manner in which evolution might alter spread velocity.

To answer our questions, we take two complementary approaches. The first combines an Evolutionarily Stable Strategy (ESS) analysis using adaptive dynamics with an analytical solution to the spread velocity in patchy landscapes (Pachepsky & Levine 2011). The second

approach uses simulations, which allow us to explore the eco-evolutionary dynamics of the invasion at intermediate gap sizes, and with a finite number of individuals. In all cases, we focus on spreading annual plant populations with a trade-off between the ability to tolerate intraspecific competition and the ability to produce offspring when rare.

METHODS

Modeling framework

We used an integro-difference equation approach to model the movement of an annual plant population through a linear environment (Kot et al. 1996; Hastings et al. 2005; Pachepsky and Levine 2011). This approach allowed us to build on previous work that developed an analytical approximation for spread velocity in patchy landscapes (Pachepsky and Levine 2011). Specifically, spread is described by the following expression:

$$N_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y)g(N_t(y)) dy \quad (\text{Eq. 1})$$

The population density at location x at time $t+1$ ($N_{t+1}(x)$) is the sum of all seeds produced at all locations y in year t ($g(N_t(y))$), multiplied by the proportion of seeds that disperse from y to x ($k(x-y)$).

The dispersal kernel (k) describes the probability a seed moves from location y to location x . We modeled dispersal with a double-sided negative exponential (Laplacian) function, which is a commonly used function describing dispersal kernels (Willson 1993). The parameter m determines the rate at which the probability of dispersal declines with increasing distance from the parent:

(Eq. 2)

$$k(x - y) = \frac{m}{2} e^{-m|x-y|} \quad (\text{Eq. 2})$$

Although our models incorporate dispersal, we do not examine the evolution of dispersal ability in the current paper, since this is the subject of numerous other studies, and there are very few cases where dispersal would not be selectively favored in spreading populations (but see e.g. Travis and Dytham 1999; Higgins et al. 2003; Schtickzelle et al. 2006; Hanski 2011).

We modeled seed production ($g(N_t(y))$) using a common annual plant population model (Watkinson 1980; Levine and Rees 2002):

$$g(N_t(y)) = \frac{\lambda N_t(y)}{1 + \alpha N_t(y)} \quad (\text{Eq. 3})$$

Here, total seed production is a function of the total number of seeds that start the generation, multiplied by the intrinsic rate of increase (λ , the per seed fecundity), which is reduced by the influence of competition from neighbors as governed by α . Thus α is the sensitivity of individuals to competition, determining the rate at which seed production declines with conspecific competitor density (Watkinson 1980), and individuals with lower sensitivity to competition (lower α) have higher competitive tolerance.

To explore how the degree of landscape patchiness changes selection on demographic rates, we assumed a trade-off between fecundity (λ) and sensitivity to competition (α) such that more competitively sensitive individuals have higher fecundity:

$$\lambda = c\alpha^d. \quad (\text{Eq. 4})$$

d is a parameter dictating the concavity of the trade-off (Figure 1), and c is a scalar used to generate realistic values of λ . Though positive in slope, this relationship between α and λ describes a trade-off, because the greater values of α (along the x -axis of Figure 1) associated with high fecundity cause greater sensitivity to competition. This general relationship follows

from the hypothesized trade-off between the ability of an individual to produce high numbers of offspring when growing at low density and its ability to cope with competitors when growing at high density. For example, annual plants commonly face a trade-off between producing a large number of small seeds, which are sensitive to competition, or a smaller number of competitively superior large seeds (Harper 1977; Turnbull et al. 1999).

The concavity of the trade-off proves an important variable in subsequent analyses of this model. When $d < 1$, increasing sensitivity to competition (increasing α) leads to diminishing returns in fecundity (λ). As is most obvious in the upper two curves of Figure 1, small increases in α from 0 lead to rapid increases in fecundity, while each successive reduction in competitive ability (increase in α) gives successively smaller fecundity gains. In the above example of seed size, $d < 1$ would arise if competitive sensitivity (α) was a more concave-up function of seed size than was low-density fecundity. In contrast, when $d > 1$, increasing sensitivity to competition leads to increasing returns in fecundity. In this case, each successive decrease in competitive ability is associated with ever-increasing fecundity gains.

Adaptive dynamics analyses

We used an adaptive dynamics approach to evaluate the evolutionarily stable value of competitive sensitivity (α) as a function of d at the leading edge of the invasion. Since fecundity (λ) is a function of competitive sensitivity, this also determines the evolutionarily stable value of fecundity. We do this only for patchy landscapes, because in continuous landscapes, the per capita growth rate (fitness) is simply the intrinsic rate of increase (λ in our models) at the front of the invasion (Holt et al. 2005; Phillips et al. 2010), where invader individuals typically do not experience intraspecific competition, except for example, when demographic stochasticity is

present (Lewis and Pacala 2000). Therefore, selection favors ever-increasing values of λ (constant directional selection) at the invasion front with this model, and no ESS exists.

To calculate the ESS in patchy landscapes, we built on an analytical approximation developed by Pachepsky and Levine (2011) for spread velocities when patches were sufficiently far apart. In this approximation, the population in the leading patch transitions between recently colonized (one individual) and a population at carrying capacity, though intermediate population sizes can also be included. Population growth and dispersal success determine the probability of transitioning between states in the leading patch, and spread velocity can be calculated from the dominant eigenvector for the Markov chain system. Importantly, this approximation closely matches simulated invasion velocities once gaps reach 3 - 4 times the mean dispersal distance (Pachepsky and Levine 2011). We assumed that except for the implicit generation of rare mutants in the adaptive dynamics approach, the strategy defined by λ and α had perfect heritability. The analytical model is described in greater detail in Online Appendix A (for code, see zip file, available online).

Simulations

Selection in patchy landscapes

The analytical ESS approach is useful for understanding the evolutionary dynamics of large populations with effectively continuous variation in density spreading through highly fragmented landscapes (those conditions for which the Pachepsky and Levine (2011) approximation is reasonable). To explore how the discrete nature of individuals and intermediate degrees of landscape patchiness influence the combination of demographic traits (λ and α) that

rise in frequency at the invasion front, we used a series of simulations. These simulations also allow us to validate the ESS results.

In our simulations, we tracked the fate of clonal individuals, each with a strategy drawn from the trade-off curve between fecundity and competitive tolerance (Figure 1), as they invaded a linear series of patches. Each suitable patch was of equal width and either directly adjacent to or separated from other patches by equal-sized gaps; patch width was half the mean dispersal distance (mean dispersal distance = 2 patches; $m = 0.5$). We explored strategies drawn from three different forms of the trade-off curve ($d = 0.4, 0.7, 1.1$, as illustrated in Figure 1). We examined two cases with $d < 1$, where increasing sensitivity to competition (increasing α) leads to rapidly ($d = 0.4$) and more gradually ($d = 0.7$) diminishing returns in fecundity (λ). We also examined the case when $d > 1$, where increasing sensitivity to competition is associated with increasing returns in fecundity. In all cases we drew 10 strategies and set $c = 80$ (Figure 1). This approach makes the necessary assumption that selection acts on standing variation within a population.

Each simulation started with 20 individuals in the first habitat patch (2 from each of 10 strategies drawn from a trade-off curve, Figure 1). In each time step, the number of seeds produced by individuals of a particular strategy (i) is reduced by competition from the total number of plants (regardless of strategy) in the patch (following from Equation 3).

$$g(N_{i,t}(y)) = \frac{\lambda_i N_{i,t}(y)}{1 + \alpha_i (\left(\sum_{j=1}^{10} N_{j,t}(y)\right) - 1)} \quad (\text{Eq. 5})$$

Plants can only make an integer number of seeds, which was achieved by rounding the total number of seeds produced by each strategy. The motivation for rounding rather than using a Poisson distribution for fecundity was to focus the results on stochasticity in dispersal only. In this discrete individual form of the model, 1 is subtracted from N in the denominator so that a solitary individual still produces λ seeds. After seed production, each seed is dispersed following

a stochastic draw from a Laplacian distribution (Equation 2). Distances were rounded to the nearest integer to assign seeds to patches or gaps, and seeds could move in either direction from their parent. Landscape boundaries were absorbing, although the landscape was long enough that seeds did not disperse beyond the furthest patch. Seeds falling in gaps died. To evaluate how the successful strategy at the invasion front depended on landscape structure, we ran 1000 replicate invasions for 40 generations each, and repeated this for 6 gap sizes (ranging from continuous to $5 \times$ mean dispersal distance) and for each of the three trade-off curves. At the end of each replicate invasion, we recorded the strategy at the leading edge.

Effects of dispersal stochasticity

Because we observed considerable variation in the dominant strategy at the leading edge of the invasion with identical parameter sets, we further evaluated how stochastic events early in the spread process dictate the long-term outcome. We hypothesized that dispersal stochasticity arising from small populations in early time steps had lasting impacts by determining which strategies were initially at the invasion front. We explicitly examined this effect by changing the initial spatial arrangement of the strategies. Specifically, we invaded a continuous landscape with two strategies (C for competitive and F for fecund), drawn from the end points of a trade-off with diminishing returns ($d = 0.4$) in fecundity with increasing competitive sensitivity (points C and F in Figure 1). We started replicate invasions by introducing individuals to two neighboring patches at the beginning of a continuous landscape, and varied the spatial order such that the first patch contained individuals of only strategy C and the second only strategy F , and vice versa (N_0 of each strategy = 5 and 10). We let the invasions proceed for 30 years, at which point we recorded which strategy was at the front of the invasion. Thirty years was long enough to reliably

detect the eventual “winning” strategy. We conducted 1000 replicate invasions for each starting position (ahead or behind) in both continuous landscapes and in patchy landscapes where gap size was $5 \times$ mean dispersal distance. All simulations were conducted in R (R Development Core Team, 2015; see zip file for sample code, available online).

Influence of evolution on spread velocity.

Finally, we explored the degree to which evolution could change the spread velocity in landscapes of varying patchiness. To do this, we first calculated the α for the strategy that would be expected before the spread process selects on traits in the population. For both native species expanding their ranges with climate change or invasive species recently introduced to new ranges, we expect the starting strategy to be that which would win in a non-spreading, well-mixed environment with large enough populations that drift can be ignored. Thus the native (stationary) range is a non-spreading environment, with no unoccupied low-density space for a fecund but poorly competing genotype to perform well (as there is for an expanding population). For competing genotypes with growth functions described by Equation 5, and a large population, the winning genotype under these conditions is that which maximizes $(\lambda_i - 1)/\alpha_i$, the fecundity of the genotype, scaled by its sensitivity to competition (Godoy et al. 2014). We compared the speed associated with this α to the speed produced in our simulated evolving invasions at different levels of landscape patchiness. To do this, we projected the speed of all strategies and compared the speed of the native range strategy to the speed of the median winning (evolved) spreading strategy (Figure 3) under different landscape configurations as determined from the prior simulations (described above in ‘Selection in patchy landscapes’).

RESULTS

Landscape patchiness qualitatively changed the demographic traits under selection in spreading populations, but this result depended strongly on the concavity of the trade-off between fecundity and competitive tolerance. For a spreading population moving through a patchy landscape with very large gap sizes, we found an evolutionarily stable strategy (ESS) for the optimal combination of α and λ for all trade-offs where $d < 1$ (Figure 2, Appendix A). With $d < 1$, increasing sensitivity to competition leads to diminishing returns in fecundity. The existence of an ESS in patchy landscapes contrasts with spread through continuous landscapes, where offspring from low-density parents at the invasion front advance the population forward. Since these furthest-forward individuals experience negligible competition, there is selection for ever-increasing values of λ (Phillips et al. 2010), even at the expense of the population becoming more sensitive to competition.

The concavity of the trade-off between fecundity and sensitivity to competition is the key variable determining whether patchy environments favor populations with lower competitive sensitivity at the leading edge of the invasion. We never found an ESS in patchy landscapes for trade-offs with d values > 1 (increasing returns in λ with increasing α , Appendix A). Mutants with greater fecundity always invade because losses in competitive tolerance are never sufficient to counterbalance fitness gains from greater fecundity. By contrast, with $d < 1$ (decreasing returns in λ with increasing α), an intermediate α exists such that higher α values are not sufficiently compensated by gains in λ while lower α values come at too great of a loss in λ (Figure 2A). In general, when departing from the ESS α , increasing α has a much lower fitness cost than decreasing α . As d approaches 1, the relationship between α and λ becomes more linear, and the marginal gains in λ continue even at intermediate to large values of α , producing a larger

ESS α (Figure 2B) and a fitness curve that only diminishes slightly for values of α larger than the ESS (Figure 2A). These results hold for differing values of λ (as determined by c in Equation 4; Figure 2B).

Because the analytical results for the ESS are limited to landscapes with very large gaps and assume a separation of timescales between ecological and evolutionary change, we employed simulations to further explore how the degree of patchiness influences the ESS and invasion speed. First, the qualitative results of these simulations match those of the analytical results, showing that in continuous landscapes, high fecundity strategies dominate the invasion front, while in increasingly fragmented landscapes, depending on the concavity of trade-off, more competitive strategies come to dominate (Figure 3). For example, when gaps are $5 \times$ mean dispersal distance, the most fecund strategy dominates when $d = 1.1$ (Figure 3C), but the most competitive strategy dominates when $d = 0.4$ (Figure 3A).

Second, we can make a quantitative comparison between the ESS α and the simulation results for populations with $d < 1$ spreading through landscapes with large gap sizes (where our ESS approach is valid). For both $d = 0.4$ and 0.7 , the ESS α matches the median winning strategy (see arrows in Figures 3A and B), though other strategies all have a chance of winning. This variability in the winning strategy is especially pronounced when $d = 0.7$ —the ESS α falls between two strategies in the simulations that won 13 and 11% of the time, which may not be surprising given the shallow fitness curve (Fig. 2A). To test whether steeper fitness curves would lead to a single dominant strategy, we explored even smaller values of d . Indeed, as d declines, the single most common winning strategy in the simulations becomes increasingly dominant (for $d = 0.4$, the lowest α strategy won 56% of the simulations, and for $d = 0.3$, the lowest α strategy

won 75% of the simulations). Increasing the number of genotypes from 10 to 30 does not change the distribution of the winning strategies in landscapes with large gaps (Online Appendix B).

Role of discrete population size

The most notable distinction of the simulation results relative to the ESS analysis is the substantial variation in the winning strategies at the leading edge (Figure 3 insets). For most scenarios, nearly all strategies had some simulation runs where they dominated at the invasion front. Of course, some variation is expected with stochastic dispersal and a finite time interval. However, we also observed strong dependence of the eventual winner on events in early time steps, suggesting that early leaders had the capacity to build on their early lead.

To explore this further, we introduced two strategies drawn from either end of the trade-off curve (strategies *F* and *C* in Figure 1), and varied the spatial order in which each was introduced to a continuous landscape. In a continuous landscape, the strategy with the higher λ (strategy *F*) should win (Figure 3), and indeed when five *F* individuals were placed one patch ahead of five *C* individuals, the *F* strategy won 80% of the time (Figure 4C). Note that the five *C* and *F* individuals, respectively, produce 101 and 107 offspring that disperse in the first time step, so that even at the very beginning of the simulation, sampling is unlikely to contribute much to variation in which strategy wins. Although the absolute lead of the *F* strategy increased through time (we ran up to 1000 years), competitive (*C*) individuals are never displaced behind the invasion front, where they instead displace *F* individuals (Figure 4A). In 20% of the runs with the same parameter values and starting conditions, the *C* strategy won. In these cases, stochastic dispersal brought *C* individuals to the leading edge in early time steps, and confronted with competition, the *F* strategy was driven extinct, almost always within 10 years (Figure 4B).

Simply reversing the spatial order in which the two strategies were introduced (and changing no parameter values) increased the percent of runs in which the C strategy eventually won from 20 to 40%, demonstrating the long-term consequences of the early invasion events. When we started the invasions with more individuals in each patch ($N_0 = 10$), which makes the initial patches more crowded, the priority effects remain, although the C strategy wins more often (C strategy won 50% when started ahead, and to 25% when started behind (of 1000 replicate invasions)).

We also explored the effect of priority effects in landscapes with large gaps, where we do not expect priority effects to arise, because the F strategy cannot “run away.” When the C strategy started in the leading patch, separated by a gap $5 \times$ the mean dispersal distance from the F strategy, it led the invasion 100% of the time after only 20 years, and the F strategy went extinct (as in Figure 4B). When the F strategy started in the leading patch, the C strategy still nearly always won, but it took much longer for it to overcome the F strategy (83% after 50 years, 94% after 200 years, with $N_0 = 5$; similar result for $N_0 = 20$.).

Influence of evolution on invasion velocity

Finally, we asked how much evolving λ and α in landscapes of varying patchiness could change the spread velocity. In the stationary range, when the population is not spreading (large, well-mixed system), the most competitively tolerant of the ten strategies wins when $d = 0.4$, because it maximizes $(\lambda_i - 1)/\alpha_i$, the fecundity of the genotype, scaled by its sensitivity to competition. By contrast, in an invasion through a continuous landscape, high fecundity-competitively sensitive strategies are selected for at the invasion front, and these are the strategies with the highest invasion velocities (Figure 5). Thus in continuous habitats, evolution

could change the invasion speed substantially, or roughly 20% with this parameter set (vertical arrow in Figure 5, continuous landscape).

In patchy landscapes, the opportunity for evolution to increase the spread velocity was much less. The low α strategies favored in patchy landscapes were nearly identical to the strategies presumed to dominate the native or non-expanding range, limiting the opportunity for evolution to increase the velocity (Figure 5, gaps $5 \times$ mean dispersal distance). As d approaches 1, however, the ESS α in a spreading population gets increasingly large (Fig. 2B), and thus evolution can once again influence the spread velocity, even in patchy landscapes. When d exceeds 1, high fecundity individuals are favored at all gap sizes (Figure 3C) so landscape patchiness cannot influence the effect of evolution on spread rates.

DISCUSSION

Populations that are expanding, whether due to shifts in climate or after introduction into a new range, are predicted to move at a rate that is governed on the most fundamental level by offspring production and the ability of those offspring to disperse away from the parent (Lewis and Kareiva 1993; Wang et al. 2002). The potential for evolution of traits that influence the spread processes is intriguing and one that is only beginning to be explored by theoretical models and field observations (Holt et al. 2005; Burton et al. 2010; Monty and Mahy 2010; Bartle et al. 2013; Kilkenny and Galloway 2013; Perkins et al. 2013; Huang et al. 2015). Our results from simulation and mathematical analysis support earlier theoretical work predicting that in continuous landscapes, reproductive traits will be favored at the invading front, while competitive ability will only be favored behind the front (Burton et al. 2010). However, here we take the important next step to make predictions about how selection will act on reproduction

versus competitive ability in heterogeneous landscapes, where favorable habitat is separated by patches of unfavorable habitat.

We find that depending on the concavity of the trade-off between low-density fecundity and sensitivity to competition, large gaps between suitable habitat can favor the rise of competitively tolerant strategies at the invasion front. Given the contrast between this result and the direction of selection in continuous landscapes, patchiness can clearly influence evolutionary trajectories in spreading populations, with implications for how much evolution increases the spread velocity. We also find an important role for stochasticity in dispersal in determining which strategy dominates at the front of the invasion. Specifically, both competitive and fecund strategies could reinforce their lead once initially ahead, leading to wide variation in the leading strategy across invasions. Here we discuss our results and their implications in the context of how we might expect evolution to proceed during an invasion and the degree to which evolution can influence the rate of spread.

Although the simulation results supported those from the analytical calculations of the evolutionarily stable strategy, they also highlighted the prominent role of stochasticity in evolving, spreading populations with finite individuals. While we can calculate the optimal strategy for a given set of conditions, stochasticity in dispersal strongly determined which strategy initially got ahead, and competitive mechanisms allowed sub-optimal strategies to reinforce their lead. In particular, fecund strategies that should lead the invasion in continuous landscapes could get pinned behind the invasion and then be eliminated by the more competitive strategy. This occurred roughly 40% of the time in our simulations when the competitive strategy was started one patch ahead, even when the evolutionarily stable strategy combined high fecundity with low competitive tolerance. Conversely, when the fecund strategy was initially

ahead, as would be expected on average, it gradually increased its lead over the trailing competitive strategy. Importantly, whether the fecund or competitive strategy ultimately won caused a roughly 10% change in the eventual spread velocity (9.5 versus 8.7 patch lengths per year, on average), highlighting the lasting impacts of initial stochastic events. The role stochasticity in dispersal plays during an invasion, especially during early time steps, has been previously recognized from a purely demographic standpoint (Melbourne and Hastings 2009), but our work is among the first to emphasize its role in determining the outcome of evolution in spreading populations (see also Excoffier et al. 2009).

The degree to which the evolution of demographic traits influenced the speed of spread depended strongly on the structure of the newly invaded landscape. More specifically, since competitive tolerance was selected for in stationary, well-mixed populations and in populations spreading through patchy landscapes, we found limited effects of evolution on the spread velocity in these landscapes (but this finding only emerged when increasing α led to strongly diminishing returns in λ). By contrast, evolution had much greater effects on spread when populations moved through continuous (or nearly so) landscapes, and high fecundity was selectively favored at the expense of reduced competitive tolerance. Of course, our findings would differ if success in the native or non-expanding range required frequent re-colonization and therefore greater low-density fecundity.

Limitations of the modeling results

Our paper is based on two modeling approaches with complementary strengths and limitations: adaptive dynamics and simulations of clonal selection. Adaptive dynamics provides an analytical solution for systems with large gaps between suitable habitat, but assumes a

separation of timescales for ecological and evolutionary change that may not be appropriate for invading populations. Though constrained to individual parameter combinations, the simulations do not suffer this shortcoming, and can incorporate stochastic effects arising from the finite nature of the individuals. The simulations can also be extended to intermediate gap sizes where we have no analytical approximation of the dynamics.

Importantly, the median results from these two approaches always matched, and often the modes did also. Unsurprisingly, the best match for trait evolution occurred when the fitness peak was steep, and landscapes contained large gaps. Cases where the quantitative match was significantly worse were explainable by processes not incorporated in the adaptive dynamics approach. As noted earlier, spatial priority effects, not possible with the adaptive dynamics approach of introducing mutants to the leading edge of the invasion, strongly affected the dynamics in the simulations. For example, these effects caused competitive genotypes to eliminate their more fecund counterparts when the latter fell behind due to stochastic events. Thus the winning strategies in simulations were more competitive than predicted by the adaptive dynamics framework, especially when the fitness landscape was quite flat (as occurs when d , the concavity parameter approaches 1).

Although our models explore evolution along a particular trade-off curve, that between fecundity and competitive tolerance, we expect landscape structure to influence the evolution of spread even when other traits, especially dispersal, evolve. In fact, while λ and α may evolve rapidly, their evolution may have a lesser effect on the spread velocity than an evolving dispersal ability, which is predicted by most theoretical models that explore evolution of dispersal in spreading populations (e.g. Burton et al. 2010; Boeye et al. 2013; Henry et al. 2013; Perkins et al. 2013). Yet at the same time, both theory and empirical evidence predict a decrease in

dispersal ability in fragmented landscapes (e.g. Travis and Dytham 1999; Higgins et al. 2003; Schtickzelle et al. 2006; Hanski 2011). How these two contrasting predictions would play out over fragmented landscapes is unknown, especially when dispersal ability trades off against other traits. In prior work examining trade-offs among multiple traits, Burton et al. (2010) found that both dispersal and reproductive ability were favored over competitive ability at the front of a population expanding through a continuous landscape. Based on the trade-offs among traits used by Burton et al. (2010), we might expect that in patchy landscapes, where we found that competitive ability is favored, dispersal ability would decline. Finally, it follows naturally from our results and prior work (Burton et al. 2010) that in populations where the same functional traits control low-density fecundity, competitive tolerance and dispersal, evolution during spread selects on all of these life history traits. A classic example involves seed size in annual plants, which is known to control trade-offs between dispersal, fecundity, and competitive ability (e.g. Stanton 1984; Turnbull et al. 1999; Cappuccino et al. 2002).

Our theoretical results come with the following caveats. First, our genetic model implicitly assumes that all genetic diversity is present at the start of spread, no mutations occur, and there is perfect inheritance. In addition, while drift in our populations can occur at the clone level, this is not equivalent to genetic drift in outcrossing populations. Thus, we anticipate that while the qualitative results should hold, if these assumptions were not realistic, the strength (or rate) of the evolutionary response would be diminished, with the exception that high mutation rates might increase evolutionary potential. Swamping effects of gene flow from the rear of the invasion or the presence of Allee effects would also slow down evolution at the invasion front (Holt et al. 2005). We focused on stochasticity in dispersal, but we expect that other forms of stochasticity, especially demographic stochasticity likely in small expanding populations, would

tend to amplify priority effects by providing alternative mechanisms for non-optimal strategies to lead the invasion. Another caveat is that we have only examined one population growth model, with Beverton-Holt density dependence. Still, we expect our general conclusions about the importance of large habitat gaps, and the concavity of the fecundity-competitive ability trade-off, to hold for other forms of density dependence. Finally, we ignore interspecific competition. Thus our results should apply for invaders that are simply better competitors than the resident native species, or are strongly niche differentiated from them, both of which would minimize the effect of the resident natives on the spreading population.

Our study assumes no Allee effect, yet may still contribute to a small but emerging literature on how evolution alters the spread of populations with inverse density dependence. As noted in our earlier work (Pachepsky and Levine 2010), the combined effects of large gaps between suitable habitat and discrete population size steepen the invasion front, just as Allee effects do. In both cases, this steepening of the front allows individuals at high density to contribute to spread. In our model, we see the evolution of competitive tolerance (low α) in populations spreading through landscapes with large gaps, a result that should also emerge in continuous landscapes when populations have Allee effects. Kanarek and Webb (2010) explored the effects of evolution on spreading populations with Allee effects using theoretical models and found adaptive evolution of the density dependence of population growth.

Empirical relevance

We found that competitive ability can be selected for at the invasion front when the landscape is sufficiently patchy (Figures 2, 3). Our prediction that landscape structure influences the degree to which competitive tolerance is favored is difficult to evaluate with past empirical

studies of invading organisms because few have examined life history traits that correspond to competitive tolerance. Still, the mechanisms explored here could explain cases where spread has not favored enhanced fecundity at the front. For example, Monty and Mahy (2010) found no difference in low-density fitness traits between core and range edge populations of *Senecio inaequidens* spanning ~150 km in France. While we do not know the role intraspecific competition played in explaining this result, this species has a mean dispersal distance of around 10 m (Monty et al. 2008), meaning that a 50 meter gap between suitable sites along its roadside habitat could induce the evolutionary dynamics modeled here. That is, as *S. inaequidens* spread through a landscape with unfavorable gaps, our models predict competitive traits would be favoured over fecundity, and thus we might not expect to see differences in low-density fecundity or other fitness traits between core and edge populations. In general, our results suggest that for terrestrial plants, which experience gaps in suitable habitat at relatively small scales owing to the inefficiency of seed dispersal, intraspecific density dependence has the potential to affect selection during spread.

We believe that two further empirical approaches could be used to evaluate the predictions of our models. First, the trade-off curve between low-density fecundity and sensitivity to competition could be parameterized with data from real plant populations, such as annuals, and further, linked to dispersal ability (e.g. Skarpaas et al. 2011). From this trade-off curve, one could predict the ESS sensitivity to competition and the shape of the fitness curve, as well as explore real trade-offs between fitness and dispersal traits. Second, laboratory experiments involving a small and short-lived organism would be particularly well-suited to evaluating the eco-evolutionary dynamics predicted by our models. For example, laboratory systems have been developed to study dispersal and spread with beetles (Melbourne and

Hastings 2009; Miller and Inouye 2012), protists (Fronhofer and Altermatt 2015), and annual plants (Fakheran et al. 2010), which could be modified to include landscapes with patches of suitable and unsuitable habitat.

Conclusion

Given that spreading plant populations commonly advance through habitats that are not continuous, landscape structure should condition our expectations for how evolution will influence both the traits that are favored at the invasion front and how much evolution can influence the invasion speed. We offer three reasons for caution when applying lessons from spread models with uniform landscapes and continuously varying density to finite populations moving through patches of favorable and unfavorable habitat. First, we have shown that selection on demographic traits can be very different depending on the degree of patchiness in the landscape. Second, depending on how similar the landscape is to the range of the non-spreading population, there may be conditions under which evolution should play a very limited role in increasing invasion speeds. Finally, given that real invasions begin with a few, finite individuals, we should expect a large influence of stochasticity on how populations evolve at the invasion front.

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FIGURE LEGENDS

Figure 1. Examples of trade-off curves between sensitivity to competition (α) and the ability to produce offspring when rare (λ) across a range of concavities (for $c = 80$). Points indicate the 10 strategies used in the simulation study ($d = 0.4, 0.7$, and 1.1); dashed line indicates $d = 1$. Effects of initial conditions were examined more closely with two strategies indicated by C (competitive) and F (fecund).

Figure 2. A) Dependence of fitness on the sensitivity to competition (α) for a range of trade-off curves (d) in a highly patchy landscape using our analytical approximation for $c = 80$ (Appendix A), where fitness was measured as the long-run per capita growth rate (Equations 1 or 2 in Appendix A). The evolutionarily stable strategy for α occurs at the fitness peak. B) Relationship between the concavity of the trade-off curve (controlled by d) and the ESS α for three levels of c (scalar for λ). In both panels, patch size = $0.5 \times$ mean dispersal distance, gap size = $5 \times$ mean dispersal distance, and $m = 0.5$.

Figure 3. Simulation results showing the distributions of winning strategies at the leading edge of 1000 replicate invasions after 40 years, across a range of gap sizes for three trade-off curves between α and λ (A) $d = 0.4$; B) $d = 0.7$; C) $d = 1.1$ ($c = 80$; $m = 0.5$). Each invasion was started with equal frequencies of 10 strategies (see Fig. 1). Points indicate the median sensitivity to competition (α) across simulation runs; histogram insets show the frequency of winning strategies (by α) for continuous landscapes (gap size = 0), and for small and large gap sizes (3 and $5 \times$ mean dispersal distance respectively); arrows indicate the location of the analytical approximation for the ESS.

Figure 4. Effects of initial conditions on which of two strategies (competitive strategy (C) or fecund strategy (F) shown in Figure 1) eventually leads an invasion through a continuous landscape. Left panels are example invasions at three time steps for an invasion started with the fecund strategy ahead (black lines = F , grey lines = C) for two cases: A) F eventually leads, and is visibly ahead by $t = 5$; B) C eventually leads and drives F to extinction, visible by $t = 8$. C) Proportion of times each strategy is at the front after 30 years. Grey shading shows the proportion of runs in which the competitive strategy (C) wins; black shows the runs in which fecund strategy (F) wins. Starting conditions included individuals in the two leftmost patches, with one strategy ahead and one behind and $N_0 = 5$ of each strategy.

Figure 5. Mean invasion velocity (number of patch lengths per year) for each strategy moving independently (drawn from trade-off where $d = 0.4$, $m = 0.5$) through landscapes with three degrees of patchiness: continuous, small gaps ($2 \times$ mean dispersal distance), and large gaps ($5 \times$ mean dispersal distance). Dashed horizontal arrows show potential increase in sensitivity to competition due to evolution (from the favored α in a mean field model to the median α from simulation studies in each landscape type). Vertical arrows show increase in invasion velocity due to this change in α .

Figure 1

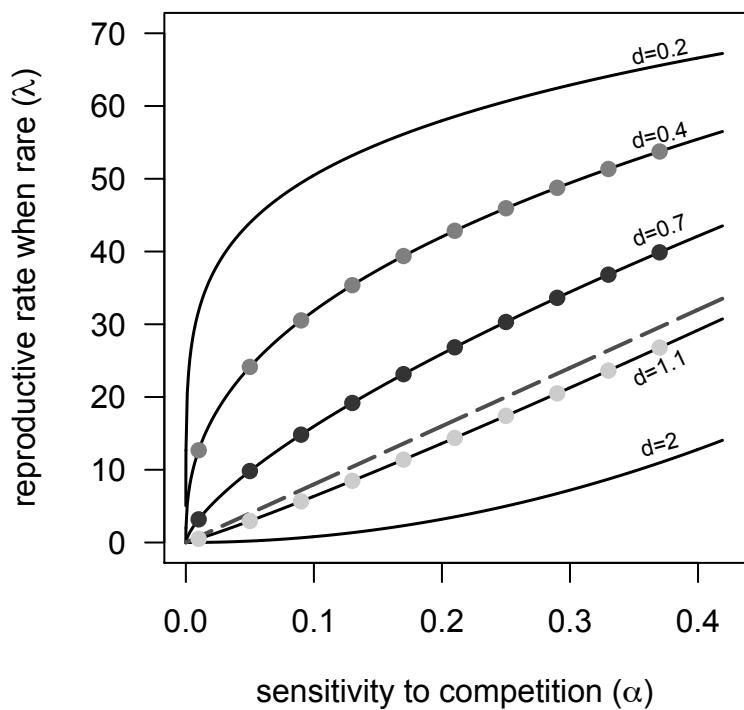


Figure 2

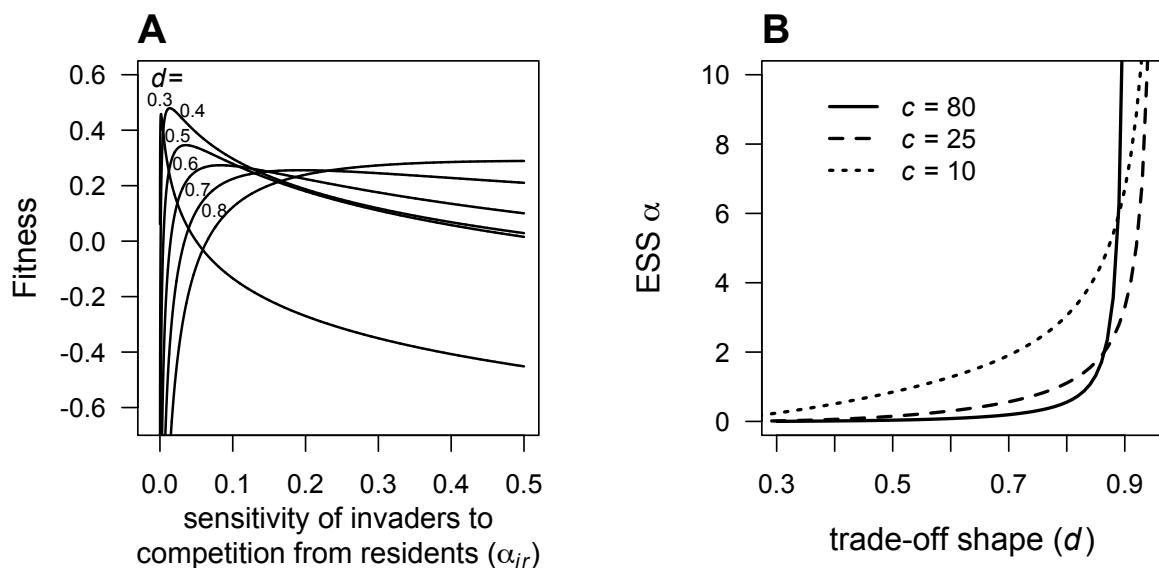


Figure 3

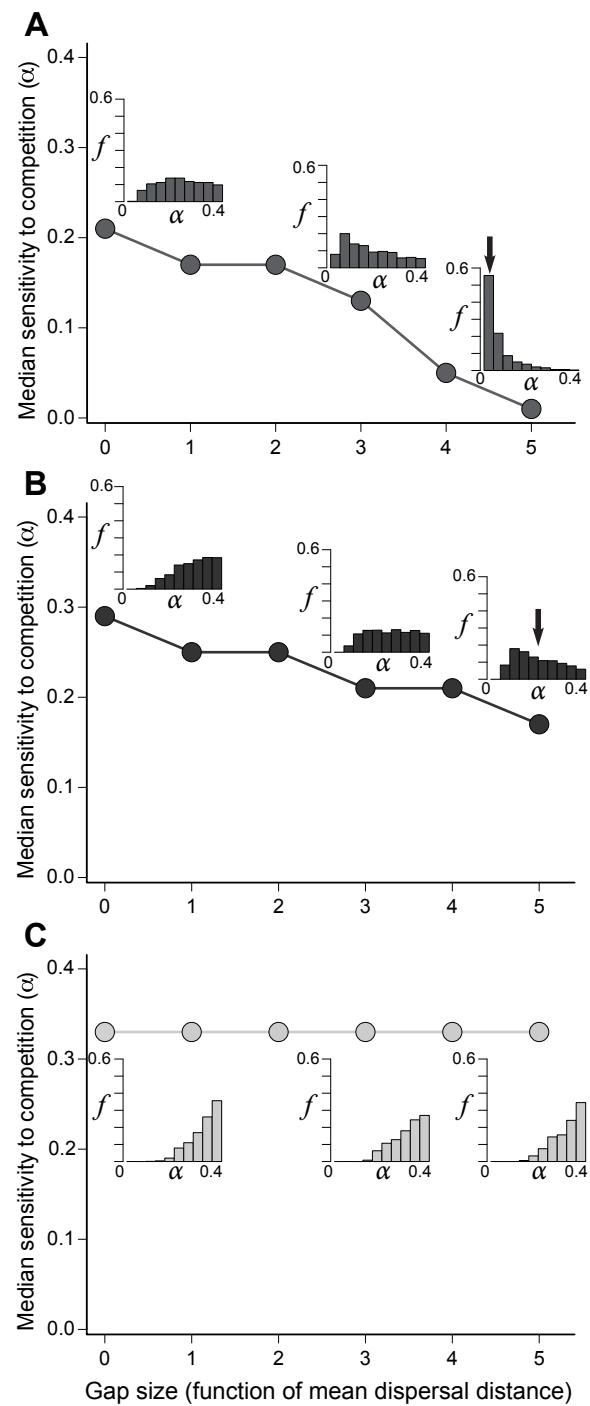


Figure 4

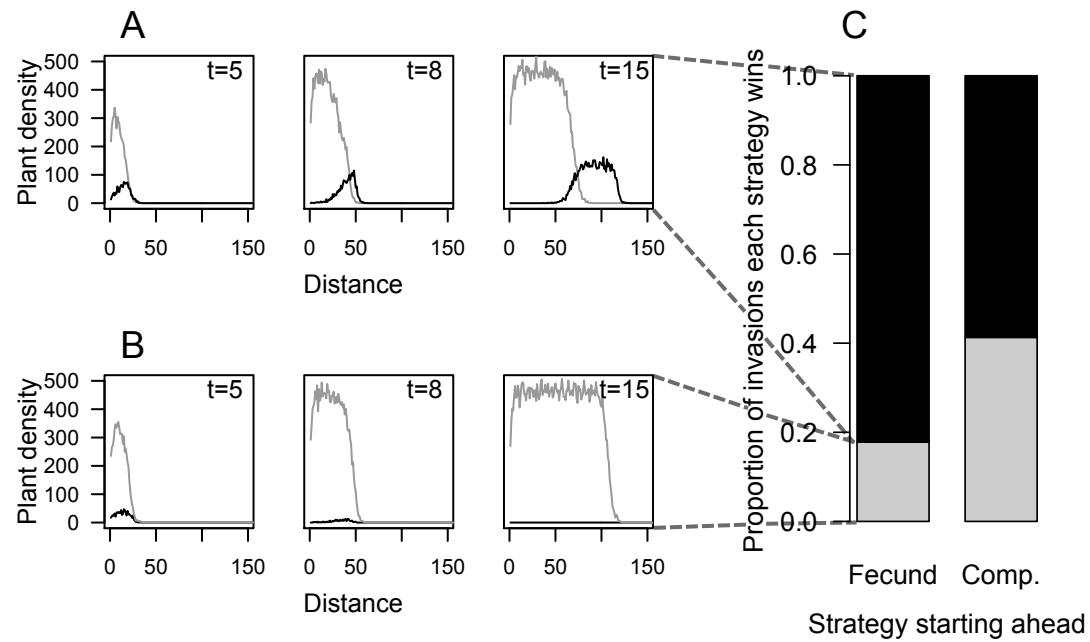
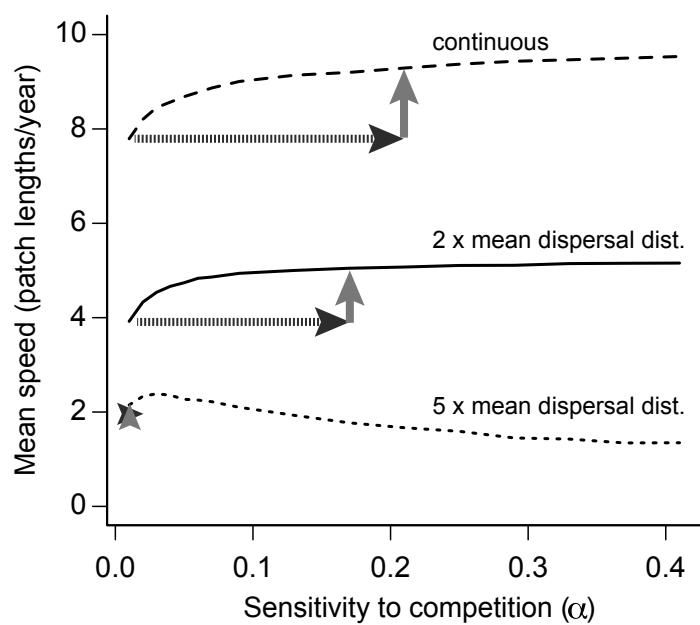


Figure 5



A Online Appendix A: Mathematical analysis

To find the evolutionarily stable state (ESS) value of the competition coefficient, α^* , we consider two competing phenotypes with different values of α . There are a small number of mutants/“invaders” while the remainder of the population consists of wild type individuals/“residents.” Residents affect invaders with competition coefficient α_{ir} and affect each other with competition coefficient α_{rr} . We assume that invaders are so rare that we can ignore competition exerted by them.

We assume that the invader is present in the leading patch. Population growth depends on population size and so invader growth varies from year to year, depending on the population of the leading patch. We define invader fitness as the invader’s long-run per capita growth rate, \bar{r}_i , which is given by the time average of the logarithm of yearly growth (Lewontin & Cohen, 1969). Thus,

$$\bar{r}_i = \sum_N q_N \ln(\text{invader growth at patch population size } N), \quad (\text{A1})$$

where the population spends q_N proportion of the time at population size N .

Rather than consider all possible population sizes, we use a 2-state Markov chain model developed in Pachepsky & Levine (2011), which we summarize here. We assume that patches are small, so that a single colonist produces enough offspring to fully populate the patch by the next time step, and that patches are far apart, so that an empty patch will receive at most a single colonist and that from its nearest occupied neighbor. Population sizes are thus either 1 or K^* , the effective carrying capacity. The Markov chain considers the state of the leading occupied patch. We reproduce Fig. B1 from Pachepsky & Levine (2011), which defines the model.

With this 2-state model, invader fitness becomes

$$\bar{r}_i = q_1 \ln(\text{invader growth at } N = 1) + q_{K^*} \ln(\text{invader growth at } N = K^*). \quad (\text{A2})$$

Let us first find the invader growth values. As described in the main manuscript, fecundity is given by $\lambda(\alpha) = c\alpha^d$. In the presence of N other individuals, competition reduces the number of seeds produced to

$$\frac{\lambda(\alpha)N}{1 + \alpha N}. \quad (\text{A3})$$

Dispersal causes some of these seeds to fall outside the patch, where they are lost. A fraction β remain in the patch, where β is the integral of the dispersal kernel from the center of the patch to the two edges:

$$\beta = \int_{-\epsilon/2}^{\epsilon/2} k(y) dy = \int_{-\epsilon/2}^{\epsilon/2} \frac{m}{2} e^{-m|y|} dy = 1 - e^{-m\epsilon/2}. \quad (\text{A4})$$

Thus, when the invader is alone, it produces a number of offspring

$$\beta \lambda(\alpha_{ir}) \quad (\text{A5})$$

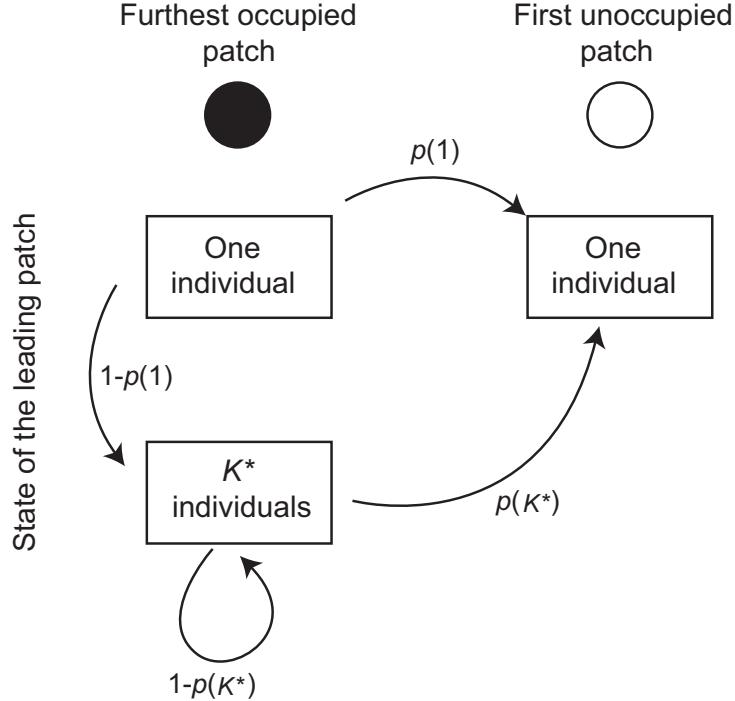


Figure A1: A just-colonized patch has 1 individual. It then either successfully colonizes the next empty patch with probability $p(1)$ or fails to colonize with probability $1 - p(1)$. If it successfully colonizes, there is a new leading patch, again with 1 individual. If it fails to colonize, it remains the leading patch, now with population K^* . This high-population patch now colonizes the next empty patch with probability $p(K^*)$ and fails to colonize with probability $1 - p(K^*)$.

and at population size $N = K^*$ (the invader plus $K^* - 1$ residents), it produces a number of offspring

$$\frac{\beta\lambda(\alpha_{ir})}{1 + \alpha_{ir}(K^* - 1)}. \quad (\text{A6})$$

The effective carrying capacity K^* is the number of seeds in a patch at equilibrium. The equilibrium condition is

$$K^* = \frac{\beta\lambda(\alpha)K^*}{1 + \alpha(K^* - 1)}, \quad (\text{A7})$$

and the effective carrying capacity is thus

$$K^*(\alpha) = \frac{\beta\lambda(\alpha) - 1}{\alpha + 1}. \quad (\text{A8})$$

Given this 2-state model, invader fitness is given by

$$\bar{r}_i(\alpha_{ir}, \alpha_{rr}) = q_1 \ln(\beta\lambda(\alpha_{ir})) + (1 - q_1) \ln \left(\frac{\beta\lambda(\alpha_{ir})}{1 + \alpha_{ir}(K^*(\alpha_{rr}) - 1)} \right). \quad (\text{A9})$$

Note that the effective carrying capacity K^* is determined by the resident population and so depends on the resident-resident competition coefficient, α_{rr} , while the invader's fecundity, λ , depends on the invader's competition with those residents and is thus a function of α_{ir} .

Let us now find the fraction of time spent at each of these two population levels. The Markov chain transition matrix is

$$\begin{pmatrix} p(1) & p(K^*) \\ 1 - p(1) & 1 - p(K^*) \end{pmatrix}. \quad (\text{A10})$$

The fraction of time spent in each of the two states is given by the dominant right eigenvector (q_1, q_K) , where

$$q_1 = \frac{p(K^*)}{1 - p(1) + p(K^*)} \quad (\text{A11})$$

is the fraction of time spent at population 1 and $q_K = 1 - q_1$ is the fraction of time spent at population K^* .

All that remains is to find the transition probabilities $p(1)$ and $p(K^*)$. As discussed in Pachepsky & Levine (2011), the probability that a seed lands in the next farthest patch, which is a distance x_0 away, is

$$p(1) = \int_{x_0 - \epsilon/2}^{x_0 + \epsilon/2} k(y) dy = e^{-mx_0} \sinh(m\epsilon/2). \quad (\text{A12})$$

A patch with K^* residents produces N_{\max} seeds:

$$N_{\max} = \frac{\lambda(\alpha_{rr})K^*(\alpha_{rr})}{1 + \alpha_{rr}(K^*(\alpha_{rr}) - 1)}. \quad (\text{A13})$$

The probability that none of them succeed in landing in the next farthest patch is

$$(1 - p(1))^{N_{\max}} \quad (\text{A14})$$

and thus the probability that at least one does land in the next patch ($p(K^*)$) is 1 minus this:

$$p(K^*) = 1 - (1 - p(1))^{N_{\max}}. \quad (\text{A15})$$

To find the ESS value of the competition coefficient, α^* , we solve the equation

$$\left. \frac{\partial \bar{r}_i(\alpha_{ir}, \alpha_{rr})}{\partial \alpha_{ir}} \right|_{\alpha_{ir}=\alpha_{rr}=\alpha^*} = 0. \quad (\text{A16})$$

By maximizing with respect to α_{ir} ($\frac{\partial \bar{r}_i(\alpha_{ir}, \alpha_{rr})}{\partial \alpha_{ir}} = 0$), we determine the optimal invader response to resident strategy α_{rr} . By stating that this maximum occurs at $\alpha_{ir} = \alpha_{rr} = \alpha^*$, we insist that the optimal invader strategy be to adopt the resident strategy, α^* . This allows us to find a strategy α^* which is not invasible — an ESS.

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Online Appendix B: Influence of number of genotypes on simulation results

Comparison of the distribution of frequency of winning strategies in very patchy landscapes (gaps $5 \times$ mean dispersal distance) for $d = 0.4$ (top row) and $d = 0.7$ (bottom row) for simulations started with 10 strategies (left column) or 30 strategies (right column). For all panels, $N_0 = 2$ for each strategy; $c = 80$; $m = 0.5$; number of replicate invasions = 1000.

