



Trait correlations and landscape fragmentation jointly alter expansion speed via evolution at the leading edge in simulated range expansions

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Abstract

Rapid evolution during range expansion is a key mechanism influencing species' ability to colonize new habitat. Understanding how selective processes alter expansion speed is thus critical to predicting both the spread of invasive species and responses to climate change. Theory predicts evolution of increased dispersal and fecundity at the leading edge of expansions. However, these traits are often negatively correlated, and what conditions might lead to one trait being favoured over the other are unclear. Further, while most theory assumes populations spread through homogeneously favourable environments, how selective processes acting on dispersal and fecundity alter expansion dynamics in patchy landscapes is not well understood. We investigated the role of landscape fragmentation and trait correlations in determining evolutionary trajectories at the leading edge of range expansions, and how these in turn alter expansion speed. We simulated populations with heritable trade-offs between dispersal and fecundity spreading through one-dimensional landscapes with varying degrees of fragmentation. We found that, in populations with a weak trade-off, the strongest dispersers were selected for at the leading edge. However, in highly fragmented landscapes and with a strong trade-off, fecundity was instead favoured. Expansion speed was strongly correlated with dispersal ability at the leading edge at all levels of patchiness, and variation in expansion speed across replicates increased with fragmentation and trade-off strength. Our findings demonstrate that evolution induced by both landscape structure and trait correlations can alter spread dynamics, and that selective processes imposed by spread per se may not always be dominant in influencing expansion speed.

Keywords Range expansion · Spatial sorting · Trait correlation · Landscape heterogeneity

Introduction

The ability to predict how quickly species' ranges can expand, such as during biological invasions (Parmesan and Yohe 2003) and range shifts due to climate change (Pyšek and Hulme 2005), depends on understanding the mechanisms controlling expansion dynamics. Dispersal and reproduction at low density are typically considered the most influential parameters to expansion speed in the absence of Allee effects (Shigesada et al. 1986; Lewis and Kareiva 1993; Higgins et al. 1996; Kot et al. 1996; Lewis and Pacala 2000). However, expansions in nature are often faster than predicted by models relying on dispersal and fecundity

alone (Lewis 2000; Clark et al. 2001). A significant body of recent theoretical work investigating the role of evolution during spread demonstrates that rapid evolution of dispersal-related traits during range expansion, termed spatial sorting (Shine et al. 2011; Phillips and Perkins 2019; Peischl and Gilbert 2020), may increase expansion speed (Perkins et al. 2013; Miller et al. 2020). Further, spatial sorting can either increase or decrease variability in observed expansion speed across replicate expansions (Williams et al. 2019), which influences our ability to predict it in natural populations.

During range expansions through favourable habitat, theory predicts that the most dispersive individuals are the first to colonize novel habitat beyond the range edge, often resulting in assortative mating by dispersal ability (Travis and Dytham 2002). The theory is supported by a number of empirical studies showing that evolving populations spread faster than populations where spatial evolutionary processes have been suppressed (Fronhofer and Altermatt 2015;

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Williams et al. 2016a; Ochocki and Miller 2017; Weiss-Lehman et al. 2017; Szűcs et al. 2017). Although spatial sorting has been observed in natural populations of cane toads (Phillips et al. 2008; Alford et al. 2009; Lindström et al. 2013; Gruber et al. 2017; Clarke et al. 2019) and insects (Thomas et al. 2001; Merwin 2019), which implicitly include landscape structure, theoretical work often assumes populations spread through homogeneously favourable environments (Miller et al. 2020). Dispersal evolution is better understood in the context of stable range margins, where habitat isolation and spatial heterogeneity in patch quality can result in low dispersal rates (Bonte et al. 2010; Kubisch et al. 2014). In general, low dispersal ability in stable range populations has a selective advantage when habitat quality is variable over space (Hastings 1983; Holt 1985; Roff 1990; Denno et al. 2001; Hutson et al. 2001; Kao et al. 2010; Wang et al. 2016). Based on these results, spatial sorting may not be a dominant process during range expansions through patchy environments.

In addition to spatial sorting, theory predicts density-independent selection at low-density expansion fronts (Travis and Dytham 2002; Burton et al. 2010); however, expansion fronts in patchy landscapes are often not at low density. Both theoretical (Snyder 2003; Pachepsky and Levine 2011) and empirical (Williams and Levine 2018) studies have established that with discrete individuals, a stronger role for density dependence arises during spread through patchy landscapes than continuous habitat. When populations are composed of discrete individuals and gaps are large, the leading edge must build to high density for individuals to become likely to cross successfully, which is analogous to positive density-dependent dispersal. Therefore, selective processes during range expansion in patchy landscapes are likely to differ not only from theoretical expectations developed in homogeneous environments (where dispersal and fecundity are favoured over competitive ability) but also from stable range populations in fragmented environments (with natural selection against dispersal). In experimental *Arabidopsis thaliana* populations, dispersal- and competition-related traits were favoured at the leading edge in patchy landscapes more than in homogeneous environments (Williams et al. 2016a). Further, in simulated expansions, the direction and strength of natural selection shifts in patchy landscapes to favour more competitive strategies over those with high reproductive rates at low density (Williams et al. 2016b).

In many species, dispersal carries energetic, time, risk or opportunity costs which can result in trade-offs between dispersal and other life history traits (Bonte et al. 2012). For example, energetic investment in structures for dispersal carries reproductive costs in arachnids (Craig 1997; Bell et al. 2005), insects (Denno et al. 1985; Dixon and Kindlmann 1999; Hughes et al. 2003; Guerra 2011; Stevens et al. 2011; Ochocki et al.

2019) and some plants (Eriksson and Jakobsson 1999). Plants can also experience increased risk from seed predation during dispersal (Fedriani and Manzaneda 2005; Östergård et al. 2007), increasing mortality and decreasing fitness (Bonte et al. 2012). During range expansion, there is an equal chance that strong dispersers or highly fecund individuals will become dominant in leading edge populations in theory (Phillips and Perkins 2019). However, empirical research suggests that spatial sorting may be the dominant selective process in leading edge populations of species exhibiting such a trade-off, at least in the absence of environmental variation (Simmons and Thomas 2004; Deforet et al. 2019; Ochocki et al. 2019). Moreover, when there are negative correlations between dispersal, fecundity and competitive ability, theory predicts that dispersal and fecundity are favoured at the leading edge while competitive ability tends to decline (Burton et al. 2010). Although potential trade-offs do not generally alter evolutionary outcomes, the strength of such a trade-off can influence expansion speed (Marculis et al. 2020) making trait correlations an important consideration in studying expanding populations. While evolution is generally expected to increase expansion speed, it is possible for spatial sorting to decelerate invasions if there is a very strong trade-off between dispersal and reproductive ability (Ochocki et al. 2019).

Analytical models of range expansion without evolution indicate that landscape fragmentation typically slows expansions (Kawasaki and Shigesada 2007; Dewhurst and Lutscher 2009; but see Crone et al. 2019). The positive density dependence of dispersal across gaps that arises from the discretization of space can also cause expansion to become pinned or locked behind gaps between habitat patches (Wang et al. 2019). These dynamics may limit the role of evolution in speeding up expansions in patchy environments (Williams et al. 2016b). Surprisingly, however, the evolution of traits related to dispersal ability increases expansion speed more significantly in fragmented landscapes than homogeneously favourable ones (Williams et al. 2016a).

It is interesting to note that the emergence of positive density-dependent dispersal behind gaps, along with an increased role for competition at the leading edge, should make spread through patchy landscapes analogous to a “pushed wave” (Roques et al. 2015; Dohirel et al. 2021). In contrast to a “pulled wave” dynamic where individuals at the leading edge drive spread, “pushed” waves advance due to individuals dispersing from behind the wave front. Because many individuals at the front originate from the range core during pushed wave expansions, it is expected that the leading edge will have higher genetic diversity compared to “pulled” waves (Roques et al. 2012; Bonnefon et al. 2014). Thus, if patchy landscapes create “pushed” waves, we can

expect more variability in traits found at the leading edge in each replicate expansion. "Pushed" waves are also expected to have a higher velocity, with a similar periodic wave pattern found in expansions through patchy landscapes (van Saarloos 2003; Gandhi et al. 2016).

The amount, arrangement and relative quality of suitable habitat can affect a population's ability to establish and spread across patchy landscapes (Shigesada et al. 1986; Kinezaki et al. 2010; Hodgson et al. 2012). Populations can spread faster in landscapes with a higher proportion of suitable habitat (Barros et al. 2016), and higher connectivity between suitable patches can facilitate range expansion, particularly in the early spreading phase of invasive populations (Schreiber and Lloyd-Smith 2009; Morel-Journal et al. 2018). In addition, suitable patches arranged as linear channels with small gaps allow for faster expansion than highly aggregated patches between large gaps (Hodgson et al. 2012). Thus, considering both the distance between suitable habitat patches and the proportion of suitable habitat is important. Few of these studies extend their results to make predictions about evolution at the leading edge (but see Schreiber and Lloyd-Smith 2009; Barros et al. 2016), but the role of landscape configuration in driving the evolution of dispersal has been studied extensively in other contexts (Cheptou et al. 2017). In particular, the proportion of suitable habitat and spatial autocorrelation of patch types can alter the direction and strength of selection for dispersal (Hovestadt et al. 2001; Bonte et al. 2010). Hodgson et al. (2012) point out that modelling large areas of suitable habitat as arrays of smaller cells can better represent local colonization processes, which is particularly important for understanding range expansions. We take up this approach by modelling large patches as rows of smaller connected patches.

Range expansions in nature are likely to take place through landscapes that are fragmented, either by anthropogenic habitat destruction or by natural processes resulting in spatial heterogeneity. Expansions through patchy or fragmented landscapes are expected to progress differently from theoretical expectations for continuous landscapes, but the extent to which evolutionary processes differ, and how they alter expansion speed in different landscape types is still unclear. In this paper, we used simulated range expansions to determine how selective processes vary depending on the degrees of both a potential trade-off in dispersal and fecundity and habitat fragmentation, and whether differences in the strength and direction of selective processes (both natural selection and spatial sorting) influenced expansion speed. While a stronger role for spatial sorting than density-independent selection in populations with strong trade-offs between dispersal and fecundity is likely in homogeneously favourable landscapes (Ochocki et al. 2019), it is currently unknown whether these results can be applied to fragmented

landscapes. That is, when there are gaps between suitable habitat patches and dispersal across gaps is controlled by the density of individuals at the patch edge, is there instead a higher selective advantage for fecundity over dispersal ability? We addressed two questions: (1) are highly dispersive strategies selected for at the expansion front in patchy landscapes despite lower fecundity, and does the scale of fragmentation (defined by both gap size and proportion of suitable habitat) change which trait is selected for during range expansion? and (2) to what extent does variation in selective processes due to fragmentation and trait correlations affect expansion speed and variation in speed across replicate expansions?

Methods

To examine how trade-offs between dispersal and fecundity influence evolution and expansion speed, we used simulations to model the expansion dynamics for an asexually reproducing species with non-overlapping generations. We varied dispersal and fecundity following three trade-off curves representing strong, moderate and weak correlations between dispersal and fecundity (described in more detail below). We simulated populations of discrete individuals spreading across one-dimensional landscapes with varying degrees of fragmentation: continuously favourable habitat; regularly spaced small, medium or large gaps of unsuitable habitat between single suitable patches; and periodic landscapes with small, medium and large rows of suitable patches between gaps of the same length. Including a variety of patchy landscapes enabled us to examine the influence of landscape fragmentation on the strength of spatial sorting and natural selection when dispersal and fecundity are negatively correlated, and how these processes influence expansion speed depending on both the proportion of suitable habitat and distance between habitat patches.

Conceptually, our simulations are based on an integrodifference equation typically used to model species with non-overlapping generations and discrete reproduction and dispersal phases (Kot et al. 1996; Pachepsky and Levine 2011; Williams et al. 2016b). In this framework, expanding populations are described by the integrodifference equation:

$$N_{t+1}(x) = \int k(x-y) \cdot g(N_t(y)) dy \quad (1)$$

where the population at time $(t+1)$ and location x is the sum over seeds produced in all locations in generation t that disperse to location x . The functions $k(x-y)$ and $g(N_t(y))$ describe the dispersal and reproductive growth phases, respectively. Using this framework, we built a simulation model that computes first population growth then

dispersal for each successive timestep t , which we define as one generation. In contrast to an analytical integro-difference model, space was represented as discrete patches (either favourable or unfavourable).

Population growth is modelled with a Beverton-Holt equation typically used to describe seed production in annual plants (Watkinson 1980; Levine and Rees 2002; Pachepsky and Levine 2011; Williams et al. 2016b):

$$g(N_t(y)) = \frac{\lambda \cdot N_t(y)}{1 + \alpha \cdot N_t(y)} \quad (2)$$

where λ is the reproductive rate at low density, α is sensitivity to competition, and $N_t(y)$ is the population at location y and generation t . The resulting value $g(N_t(y))$ was rounded to the nearest integer to model a population of discrete individuals. Here, seed production is deterministic, but a stochastic version was found to produce similar population growth patterns, and importantly, no difference in expansion speed, in previous models using the same approach (Pachepsky and Levine 2011). As we were primarily concerned with selective rather than stochastic evolutionary processes, we modelled reproduction with perfect trait inheritance as in a clonal species (see Williams et al. 2019).

After reproduction, propagules dispersed from their natal patch according to a negative exponential (Laplacian) dispersal kernel, commonly used in integrodifference models for describing expansion speed (Kot et al. 1996):

$$k(x - y) = \frac{m}{2} e^{-m|x-y|} \quad (3)$$

where m defines the rate of decline of dispersal probability with distance between the parent patch y and the natal patch x . Dispersal was density-independent and stochastic. In our simulations, stochasticity was achieved by randomly sampling from the dispersal kernel to determine dispersal distance, and from a binomial distribution to assign a random direction (forward or backward). Results were rounded to the nearest integer value in order to assign propagules to discrete habitat patches. The negative exponential kernel best represents passively dispersed species with one dispersal event that move at a constant speed and with a constant stopping rate. It is representative of dispersal processes for many plant species (Willson 1993; Clark et al. 2005) and some insects (Chapman et al. 2007; Carrasco et al. 2010; Robinet et al. 2019)-- groups that often exhibit trade-offs in reproduction and dispersal. We assumed no competitive interactions occurred in the natal patch, and no dispersal-induced mortality. Individuals that landed in unsuitable patches did not reproduce.

We predicted that strong dispersal ability would be less advantageous at the leading edge if there was a strong negative correlation with fecundity regardless of landscape

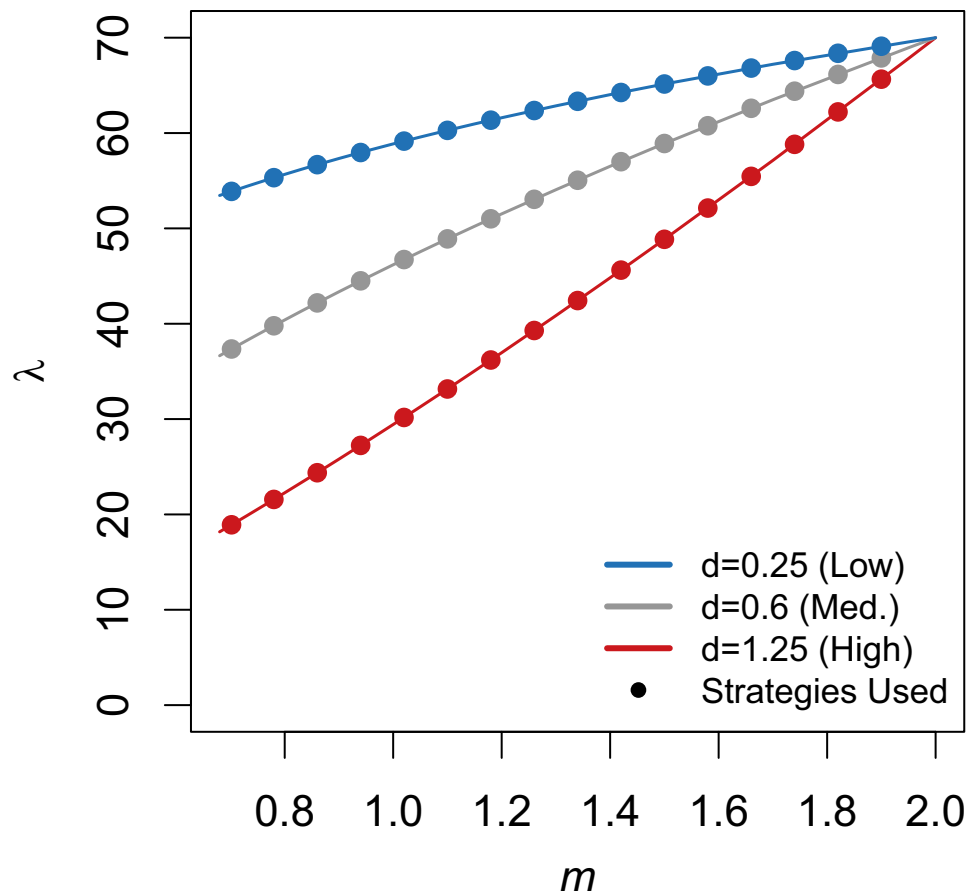
type, and thus, spatial sorting may occur less frequently in these populations, as was demonstrated in modelled cane toad populations (Chan et al. 2015). To investigate this, we assumed a trade-off curve similar to that used by Williams et al. (2016b), adapted to represent a trade-off between the parameter defining the shape of the dispersal kernel (m) and the reproductive rate at low-density (λ):

$$\lambda = c \frac{m^d}{M} \quad (4)$$

where M is the maximum value of m , the shape of the trade-off curve is defined by d , and c is a constant that corresponds to the maximum λ value. In our three trade-off curves, $c = 70$. We let m vary between 0.7 and 2 and thus set $M = 2$. As dispersal ability increases (i.e. when m decreases), the low-density reproductive rate (λ) decreases. The rate of decrease in fecundity with increased dispersal ability depends on the concavity of the trade-off curve. Three curves were selected as representative of a gradient of curves for d between 0.1 and 1.5, at $d = 0.25$, $d = 0.6$ and $d = 1.25$, representing a weak, moderate and strong trade-off, respectively (see Fig. 1). Selected results for the expanded gradient of curves, as well as an additional parameterization of the trade-off, are presented in the electronic supplemental material (ESM1 Figs. S1–S4). Populations were composed of individuals drawn at equal frequency from 16 strategies (strategy one being the most dispersive, to strategy 16 the most fecund) along each trade-off curve, evenly spaced within the range of m (shown in Fig. 1), which then were allowed to sort during spread.

Landscapes consisted of one-dimensional arrays of discrete habitat patches where each patch had independent population growth and dispersal, mimicking neighbourhoods. That is, even in landscapes with rows of connected suitable patches, population growth depended only on the individuals in the same patch, and individuals were able to disperse to any patch regardless of density. In addition to continuously favourable arrays of patches, we considered two scales of fragmentation in patchy landscapes: one where single habitat patches are placed between unsuitable gaps (that varied in length), and the other where n suitable patches are evenly spaced between gaps of length n . In this second type, the proportion of suitable habitat is constant at 50%, and populations can spread across suitable habitat to reach an edge-patch before spreading across a gap. We considered gaps of size four, six and eight patches with each patchy landscape type. As dispersal ability varied in the populations, gaps could not be parameterized to the mean dispersal distance of the population in a meaningful way, but we did consider the relationship between the range of dispersal kernels and gap lengths. The smallest gap length (four)

Fig. 1 Trade-off curves representing strong (red), medium (grey) and weak (blue) trade-offs between parameters for the growth rate at low density (λ), used in the population growth function, and the shape of the dispersal kernel (m). Note that lower values of m correspond to greater dispersal ability. Points are the 16 strategies chosen for simulations



is 2.8 times the mean dispersal distance of the most dispersive strategy, and 7.6 times the mean dispersal distance of the least dispersive strategy. The largest gap length (eight) is 5.6 times the mean dispersal distance of the most dispersive strategy and 15.2 times the mean dispersal distance of the least dispersive strategy. Therefore, we expect that most strategies will be able to cross the smallest gaps, but that as gap size increases, the advantage to the strongest dispersers in their ability to cross large gaps will also increase.

We ran 1000 simulations of 40 generations of spread per trade-off curve and landscape type. Populations of three individuals from each strategy (48 individuals total) were initialized in the left-most habitat patch. We recorded the number of patches colonized each generation and the number of individuals from each strategy present in each patch after 40 generations of spread. Expansion speed was considered both in terms of the average number of patches colonized per generation and the position of the right-most colonized patch after 40 generations. To make inferences about the relative strength of spatial sorting and natural selection at the expansion front, we recorded the distribution of strategies at the leading edge across replicates. For patchy landscapes, we also differentiated between leading edge

populations for expansions that progressed beyond the first gap vs. those that did not in order to consider the effects of selective processes on expansion extent. Simulations were conducted in R, version 3.5.3 (R Core Team 2019); original simulation code is archived on Zenodo (<https://doi.org/10.5281/zenodo.4552551>).

Results

Evolutionary outcomes

In simulations of expansions through linear landscapes, the direction and strength of selection (natural selection vs. spatial sorting) strongly depended on the strength of the trade-off between dispersal and fecundity. We found that the degree of fragmentation changed the dominant evolutionary process at the expanding edge, but only when there was a strong trade-off between dispersal and fecundity. When dispersal and fecundity were very negatively correlated, spatial sorting was the dominant process at the leading edge in homogeneously favourable landscapes, where the most dispersive strategy was found at the

leading edge in 46% of simulations (Fig. 2a). However, natural selection for fecundity was much more common in highly fragmented landscapes, and the most dispersive strategy (1) was found at the leading edge less than 1% of the time (Fig. 2c). In contrast, in all simulations of populations with a weak trade-off, dispersive strategies were found at the leading edge with high frequency spreading through all landscapes with gaps between rows of suitable patches of the same length (vs. single patches between larger gaps). In homogeneously favourable landscapes, all expansions were led by the most dispersive strategies (1–4), and these strategies also led over 90% of expansions in landscapes with rows of eight suitable patches between gaps of length eight. Intermediate strategies (5–12) were rare at the leading edge across landscape types and trade-off curves, and were present in just 13% of simulations. Across a wider range of d values, intermediate strategies were never favoured. Rather, strategies at the leading edge shifted from dispersive to fecund at $d = 1$ in our trade-off function, but at lower values for an alternative trade-off parameterization (ESM1, Fig. S2).

Expansion speed

When there was a strong trade-off (that is, when strong dispersers had low fecundity) expansions were slower than

in populations with a weak trade-off, but this difference was not as apparent as the differences based on gap length and dispersal strategy (Fig. 3e). However, there was a more pronounced decline in expansion speed with increasing trade-off strength in patchy landscapes (ESM1 Fig. S3). In landscapes with gap of length eight, the median extent decreased from 60 patches in populations with a weak trade-off to seven patches with a strong trade-off. In addition, in populations with a strong trade-off, only 20% of expansions advanced beyond the first 8-patch row in the most highly fragmented landscape (Fig. 2c), compared to 92% when the trade-off was weak (Fig. 2c).

We found that increasing gap size between suitable habitat patches slowed expansions on average (Fig. 3c). In homogeneously favourable landscapes, the median extent was 242 patches; this declined to 96 patches when gaps were six patches long, and to seven patches for length eight gaps. Expansions were slower when there were single patches between gaps than in landscapes with connected rows of suitable patches (single patches median = 48, rows median = 153) and were less likely to cross the first gap in habitat (see Fig. 2c, d). The number of patches before a gap also influenced the strength of spatial sorting, and in expansions that succeeded in crossing gaps, a higher proportion was led by fecund strategies in single patch landscapes (Fig. 4).

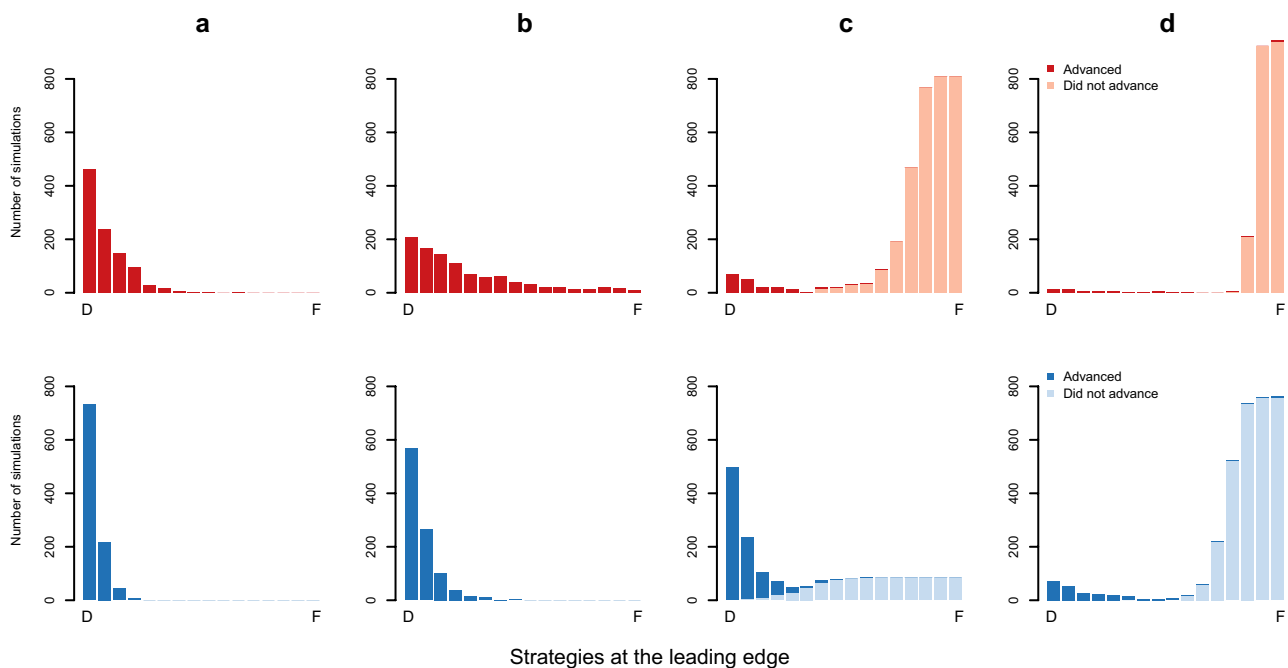


Fig. 2 The distribution of dispersal strategies at the leading edge across simulation sets in : **a**) homogeneously favourable landscapes, **b**) length four gaps between rows of 4 patches, **c**) length eight gaps between rows of eight patches and **d**) single patches between length 8 gaps. Strategies are arranged from most dispersive on the left to most

fecund on the right. Populations with strong negative correlations between dispersal and fecundity are shown in red; weak correlations are in blue. Lighter tones are those that failed to advance beyond the first gap in suitable habitat

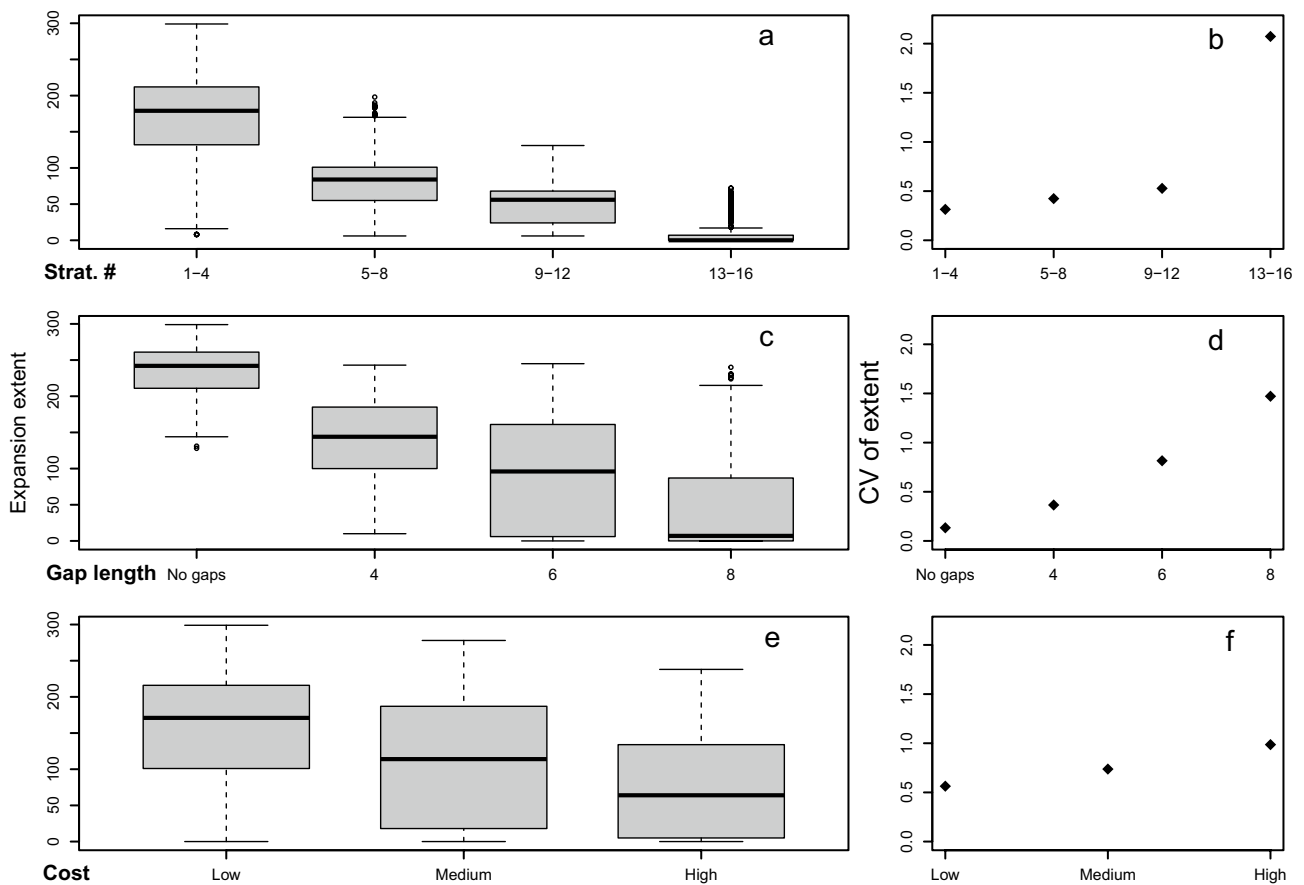


Fig. 3 Expansion speed and variation in speed across simulation sets. Boxplots in the left column (**a**, **c**, **e**) show the distribution of the final extent of simulations after 40 generations of spread; on the right (**b**, **d**, **f**) are corresponding coefficients of variation for extent. These are

shown by dispersal strategy mode (**a**, **b**), where strategy 1 is the most dispersive, 16 is the most fecund; gap length (**c**, **d**); and strength of the trade-off (**e**, **f**) and binned into groups of four to simplify visualization

Although expansions were slower through the most highly fragmented landscapes, expansion speed was more strongly influenced by the dispersal strategy at the leading edge than by gap size (Fig. 3a). The four most dispersive strategies (with $m < 1$) spread farther on average (median = 179 patches) than less dispersive strategies (median = 7 patches, strategies 5–16) regardless of landscape type, which is strong evidence that evolution of dispersal is a key driver of expansion speed independent of fragmentation. The median expansion extent declined with dispersal ability: the median extents of intermediate strategies were 84 patches (strategies 5–8) and 56 patches (strategies 9–12), while the most fecund strategies (13–16) tended to stay in the initial patch. Despite this, there was still overlap in the distribution of extent, particularly in the intermediate strategies (Fig. 3a). In addition, dispersive strategies (1–4) spread as far on average in patchy landscapes as less dispersive strategies (5–16) spread in homogeneously favourable ones (medians = 160, 163

patches, respectively). The average dispersal ability at the leading edge was also a reliable predictor of whether range expansion occurred beyond the first gap in suitable habitat (Fig. 2c, d), with successful invasions almost always led by dispersive individuals.

Expansion variability

Expansion variability, the difference in speed across replicate expansions, was strongly positively correlated with gap size and slightly correlated with dispersal strategy and the strength of the trade-off (Fig. 3 b,d,f). Homogeneous landscapes had the smallest amount of variation in extent, regardless of the trade-off curve or the dispersal ability of leading edge populations. Expansion variability increased roughly proportionally with gap length (no gaps CV = 0.13, length 4 gaps CV = 0.37, length 6 gaps CV = 0.82, length 8 gaps CV = 1.47). Variation in extent among the most dispersive strategies was also low, and similar to

Fig. 4 Bars show the number of simulations where each strategy was found at the leading edge, excluding those where populations did not advance beyond the first gap. Strategies are ordered from most dispersive (left) to most fecund (right). Dark bars are expansions through landscapes with rows of suitable patches between gaps, and light bars are single suitable patches between gaps

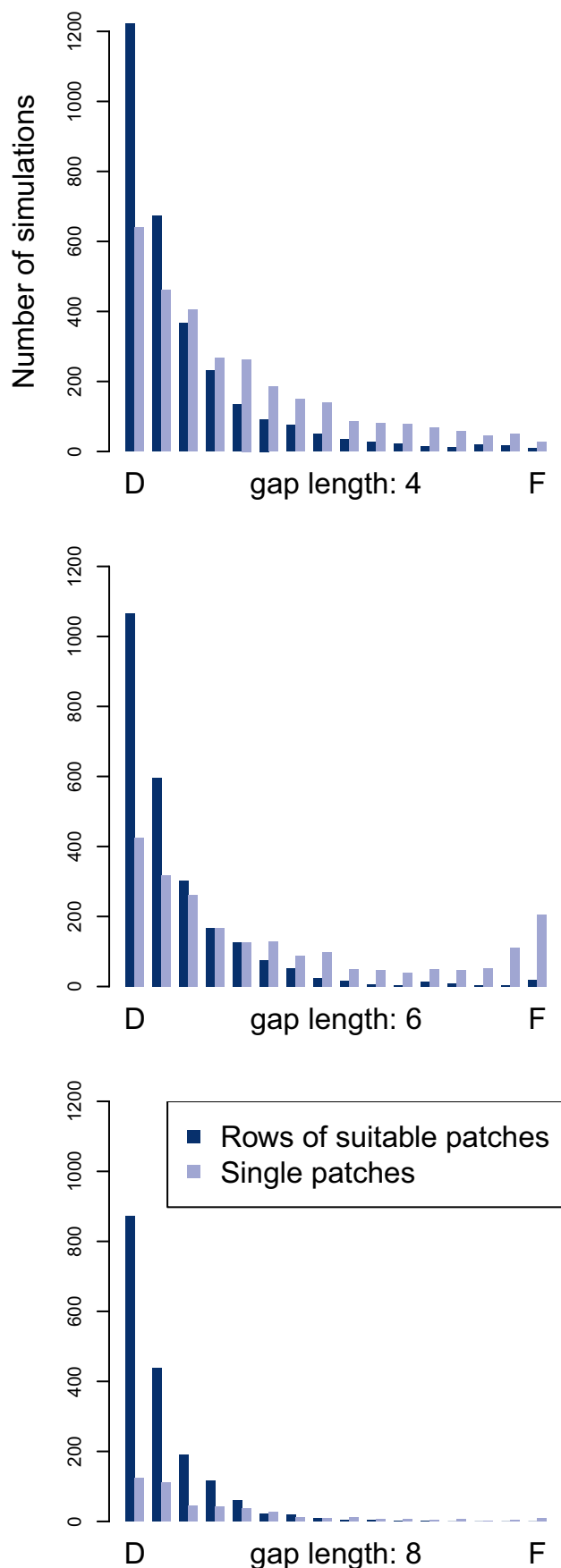
intermediate strategies (1–4 $CV = 0.31$, 5–8 $CV = 0.42$, 9–12 $CV = 0.52$). However, the four most fecund strategies had much higher variability ($CV = 2.07$) due to outliers that spread successfully across gaps (a large majority of strategies led by fecund individuals did not advance beyond the starting patch). Expansion variability also increased proportionally with the strength of the trade-off; populations with a weak trade-off had much less variability in speed than populations with a strong trade-off (weak trade-off $CV = 0.56$, moderate trade-off $CV = 0.74$, strong trade-off $CV = 0.99$). Supplemental simulations demonstrated that expansion variability in patchy landscapes depended strongly on trade-off strength, while there was a minimal effect in continuous landscapes (ESM1 Fig. S3).

Discussion

Our results highlight how evolutionary processes and landscape fragmentation can jointly influence success, speed and variation in expanding populations. With negative correlations between fecundity and dispersal, we found selection for both dispersal (spatial sorting) and fecundity (natural selection) in patchy landscapes, but the dominant selective process and its strength varied depending on the magnitude of the trade-off and the landscape structure. Expansion speed was strongly influenced by dispersal at the leading edge, but expansion variability, or the variation in speed across replicates, depended more on the length of unsuitable gaps and the strength of the trade-off. Here, we discuss these results in relation to previous theoretical and empirical work and suggest avenues for extensions to future theory as well as applications to field research.

Evolutionary outcomes

We found that, during range expansion, strategies with low dispersal ability were more often found at the leading edge in populations spreading through patchy environments, particularly when there were only single patches between large gaps, which is in line with theory for stable range populations (Hastings 1983; North et al. 2011). In contrast, in our simulations, dispersive strategies were still often favoured at the leading edge when the trade-off was weak. From metapopulation theory, we expect that a reproductive cost to dispersal will strengthen selection against dispersal



in patchy environments (Parvinen et al. 2020). Our results suggest that, in spreading populations, correlations between dispersal and fecundity can control not only the strength, but the direction of selection. Populations with a weak negative correlation (or perhaps no correlation) between dispersal and fecundity may exhibit spatial sorting even in environments where we would expect natural selection against dispersal, such as in those with a high degree of fragmentation. In climate-induced range shift scenarios, this effect can rescue a population from extinction (Boeye et al. 2013); so, understanding dispersal trade-offs within species may be of particular importance in predicting their resilience to climate change.

We expected that spread in patchy landscapes would exhibit a “pushed wave” dynamic, characterized by higher population densities and trait diversity at the leading edge (Dahirel et al. 2021; Miller et al. 2020). While the demographic profiles of our simulations in patchy landscapes did resemble pushed waves, the evolutionary outcomes fit less clearly into this framework. We found much more variation in traits at the leading edge in patchy landscapes, both within and across simulated expansions. However, this was not the case when excluding those replicate expansions that never advanced beyond the first gap. In these successful expansions, there was rarely more than one strategy present at the leading edge regardless of the landscape configuration. While dispersal across large gaps was analogous to positive density-dependent dispersal (as populations needed to build to high density for the probability of dispersing across gaps to be realized), they also amplified the role of founder effects. That is, since gap crossing was rare, it was very unlikely for multiple strategies to successfully establish beyond each gap. In sum, unlike during spread across environmental gradients (Garnier and Lewis 2016), and when dispersal is explicitly density-dependent (Birzu et al. 2019), the spatial genetic structure that arises in expansions through patchy landscapes may not be well described by the pushed wave dynamic.

Previous work has demonstrated that competitive ability is selected for over fecundity in leading edge populations spreading through highly fragmented landscapes (Williams et al. 2016b), and this could have driven selective processes in our simulations as well. Fecundity was implicitly associated with carrying capacity in our seed production function (see Fig. 5), and thus, fecund strategies were also more competitive at high densities. An implication of this association is that, if more fecund individuals disperse beyond the leading edge by chance and produce a large number of propagules who remain in their natal patch, more dispersive individuals entering the patch in later generations are likely to be unable to compete. We suggest this as a mechanism that limited the success of intermediate strategies: these strategies were unable to

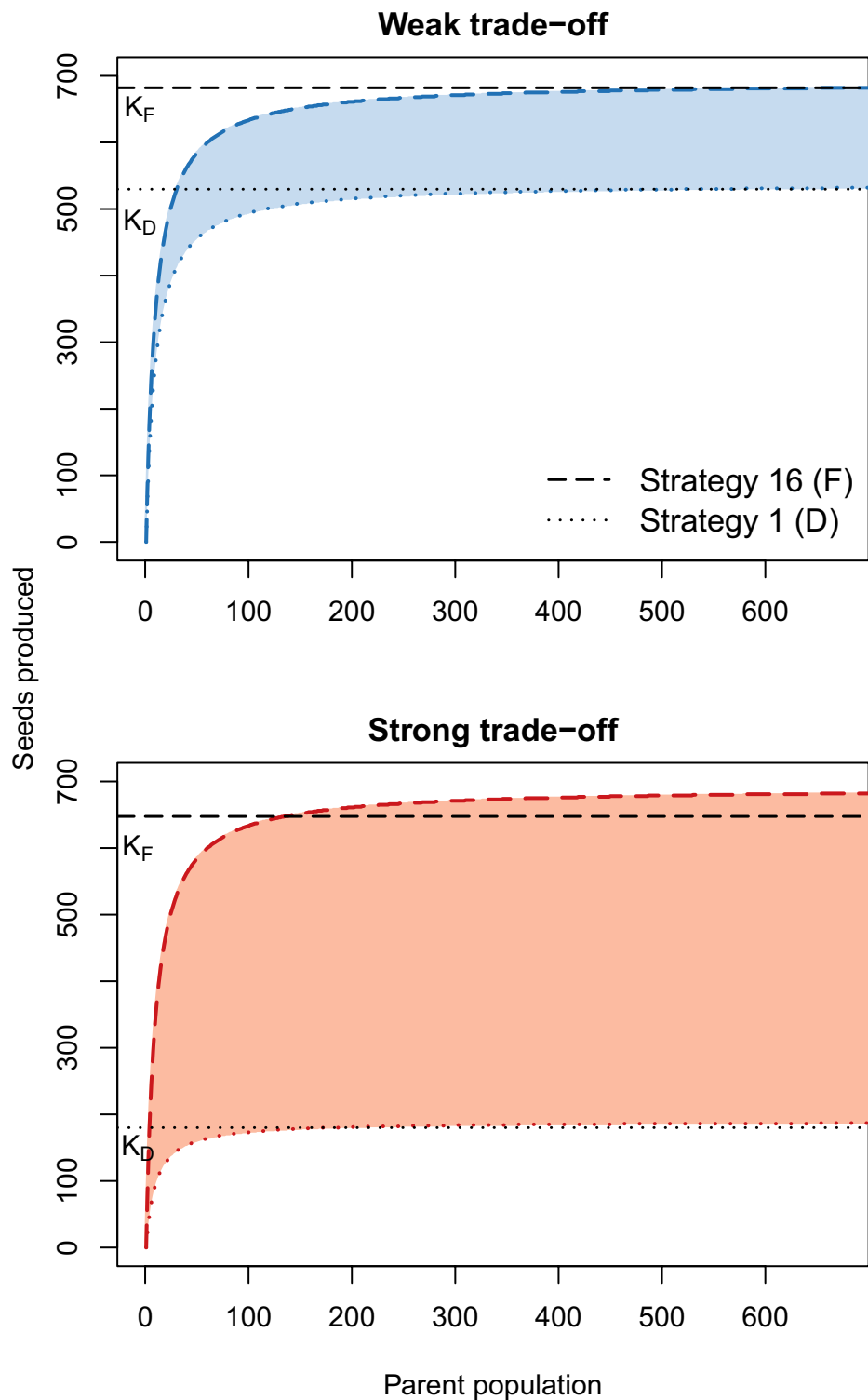
disperse beyond the leading edge and then were unable to compete with more fecund strategies that could grow to higher densities. Our model results suggest that, with a strong trade-off, there is selection against dispersal in fragmented landscapes, which we would expect given the large body of evidence that fragmentation induces selection against dispersal (see, for example, Cheptou et al. 2017). Even so, it is possible that this is confounded with selection for increased competitive ability at high density.

Expansion speed

As in our simulations, evolution of increased dispersal ability at the leading edge has been shown to increase expansion speed both experimentally (Fronhofer and Altermatt 2015; Williams et al. 2016a; Ochocki and Miller 2017; Weiss-Lehman et al. 2017; Szűcs et al. 2017) and in theory (Travis and Dytham 2002; Phillips et al. 2008; Travis et al. 2009; Burton et al. 2010; Perkins et al. 2013; Phillips 2015). With a negative correlation between dispersal and fecundity, spatial sorting was the dominant process in homogeneously favourable landscapes in our simulations, a result previously demonstrated in theory (Marculis et al. 2020) and in experimental beetle populations (Ochoki et al. 2019). In both cases, dispersal evolution was associated with faster rates of spread, and populations with strong negative trait correlations were slower. By incorporating habitat fragmentation, we revealed an even stronger link between evolution and expansion speed, in that landscape structure altered the evolutionary outcomes at the leading edge which in turn altered expansion dynamics.

While expansions through highly fragmented landscapes moved more slowly on average, we were surprised to find that large gaps did not significantly slow expansions when the leading edge was made up of dispersive individuals. It is generally accepted that expansions should progress more slowly through patchy landscapes (but see Crone et al. 2019), but our results suggest that natural selection for fecundity at the leading edge in fragmented landscapes can amplify the effect of large gaps between habitat patches on speed. In our simulations, expansions led by fecund strategies rarely advanced beyond the starting patch, but this occurred almost exclusively in highly fragmented landscapes. Meanwhile, populations that exhibited spatial sorting in highly fragmented landscapes were able to spread successfully and at a much faster speed, indicating that spatial sorting may be a necessary feature of spread in some landscapes but less influential in others (see Fig. 4). In our simulations, strong dispersal was less common at the leading edge of expansions in single-patch landscapes regardless of gap size, and fecund strategies were more successful at crossing gaps than in landscapes with rows of suitable patches.

Fig. 5 The number of seeds produced by parent populations for the strong trade-off in red, and weak trade-off in blue (see Fig. 1). The most dispersive strategy is shown with a dotted line, the most fecund with a dashed line. All intermediate strategies of seed production are contained in the solid colour area. Calculated carrying capacities for the extreme strategies are shown with horizontal lines



Expansion variability

We found that expansion variability reflected the variability in trait distributions at the leading edge, similar to previous

findings (Phillips 2015), but our results expand this association to include landscape structure. The association between gap size and variation in speed across replicates is reflective of selective processes, in that there was more

variation in strategies at the leading edge when gaps were large. In homogeneously favourable environments, where dispersive strategies dominated at the leading edge, there was only a small role for founder effects and thus little variation in speed. As the distance between suitable habitat patches increased, so did both the strength of natural selection acting on fecundity (or perhaps against dispersal), and the variability in speed. We attribute this increased variability in speed to founder effects playing a stronger role in patchy landscapes, particularly in crossing gaps. Most expansions in landscapes with large gaps were led by fecund individuals, with expansion speeds close to zero. In contrast, when dispersive strategies reached the leading edge early in the expansion, those populations spread much further, leading to a bimodal distribution of expansion speed corresponding to the binary evolutionary outcomes. It is worth noting that, in patchier landscapes, the possible distances travelled are reduced at habitat edges—individuals can only stay in the natal patch or disperse across the length of the gap. However, this outcome likely reflects dispersal across barriers in fragmented landscapes and may be relevant even when there is some small probability of colonizing in between patches. Thus, it is possible that our ability to predict expansion speed in natural populations decreases with the degree of fragmentation. This highlights the importance of expanding simulation studies of range expansions to include landscape structure, as results from field experiments may represent only one possibility of a large set of potential outcomes.

Limitations and extensions for future research

While our results are generalizable to populations with genetically based trade-offs between dispersal and fecundity in a variety of landscape types, they rely on a number of assumptions which suggest avenues for future research. Our model considers dispersal, fecundity and competitive ability to be perfectly inherited from parent to propagule and does not include mutation, which could influence evolutionary outcomes. Perfect inheritance also removes the role of recombination, which is hypothesized to introduce a larger role for stochastic evolutionary processes in leading edge populations (Williams et al. 2019) but could also give selection more material on which to act (Otto 2009). Therefore, incorporating mating and recombination is worth future investigation. Our focus has been on deterministic evolutionary processes, but we cannot exclude stochastic processes such as genetic drift and gene surfing from influencing our results. For example, a strong founder effect early in expansions has been found to dictate strategies at the edge for many generations of spread (Williams et al. 2016b).

Our trade-off function assumed that the population mean λ declined with increasing trade-off strength. We expect that

the correlation between trade-off strength and variability in leading edge strategies we found does not rely on this assumption. In supplemental simulations where only the population mean reproductive rate varied (and trade-off strength did not), we found more variability in winning strategies for high- λ populations in patchy landscapes (ESM1 Fig. S4), the opposite of what we would expect if the differences in λ between our curves were driving this result. In addition, the median strategy at the leading edge was slightly more fecund in both continuous and patchy landscapes (ESM1 Fig. S4), indicating that, with increased mean λ , the trade-off strength amplified this difference in patchy landscapes. The sharper decrease in speed and increase in variability in patchy landscapes was not found in an alternative trade-off parameterization where trade-off strength varied less than mean λ , but we did find that reducing mean λ alone produced the same qualitative patterns in expansion speed and variability that we found between trade-off curves (ESM1 Figs. S3–S4). So, it remains unclear how the difference in mean λ across curves may have influenced these specific findings. As expansion speed and variability were more strongly affected by the evolutionary outcomes at the leading edge and by landscape type than by the trade-off itself, we expect our results will generalize beyond the assumption that reproductive rate decreases with increasing trade-off strength.

We assumed that the mean dispersal distance varied in populations, but not the shape of the kernel itself, which can also be under selection (Starrfelt and Kokko 2010). Incorporating long-distance dispersal events through varying the tail-shape of the dispersal kernel would alter expansion dynamics, particularly in fragmented landscapes (Fayard et al. 2009; Lindström et al. 2011). Similarly, while our choice of the Beverton-Holt function for density-dependent growth allowed us to control for the sensitivity to competition (α), a parameter that is under selection in our model (Williams et al. 2016b), an alternative growth model would allow a more thorough exploration of the role of carrying capacity (K) and competitive ability (α) in each strategy's ability to colonize the leading edge. Setting a constant carrying capacity and allowing α to vary may alter selective pressures by reversing implicit correlations between dispersal and fecundity, the two traits we consider here, with competitive ability. However, an alternate parameterization would not allow us to deconfound competition-related traits from fecundity, and thus, it is not possible in our model to discern whether selection against dispersal or selection for other life history traits (fecundity or competitive ability) at high density was the dominant process at the leading edge in highly fragmented environments. Considering the interaction of competition and dispersal in expansions through patchy environments presents an interesting direction for future research.

Conclusion

Most range expansions in nature occur through patchy and fragmented landscapes, and our results provide further evidence that landscape structure should not be ignored when developing theory for eco-evolutionary processes during range expansion. Habitat fragmentation may fundamentally alter the ability of populations to spread, particularly in species with strongly negative correlations between dispersal and reproductive output. Our findings that populations with weak trade-offs were much more likely to spread even in highly fragmented landscapes suggest that correlations between dispersal and other traits may influence a species' invasiveness in patchy landscapes, and that understanding trait associations may help us to predict range expansions in the field. Similarly, since the influences of landscape structure and evolution on expansion dynamics cannot be easily separated, considering the combined influence of intrinsic and extrinsic factors on expansion speed is necessary in advancing our understanding of the dynamics of range expansion.

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Code availability R code for the simulation model and processing its results is available at <https://doi.org/10.5281/zenodo.4552551>.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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