

LETTER

Trade-offs and the evolution of life-histories during range expansion

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Abstract

During range-advance, individuals on the expanding edge of the population face a unique selective environment. In this study, we use a three-trait trade-off model to explore the evolution of dispersal, reproduction and competitive ability during range expansion. We show that range expansion greatly affects the evolution of life-history traits due to differing selection pressures at the front of the range compared with those found in stationary and core populations. During range expansion, dispersal and reproduction are selected for on the expanding population front, whereas traits associated with fitness at equilibrium density (competitive ability) show dramatic declines. Additionally, we demonstrate that the presence of a competing species can considerably reduce the extent to which dispersal is selected upwards at an expanding front. These findings have important implications for understanding both the rate of spread of invasive species and the range-shifting dynamics of native species in response to climate change.

Keywords

Competition colonization trade-off, environmental change, individual-based model, migration, phenotype evolution, range margin, rapid evolution, stochastic simulation model.

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INTRODUCTION

The majority of evolutionary and ecological theory assumes that species' ranges are stable in space. However, many key processes in ecology and evolution clearly violate this assumption. Subjects ranging from historical biogeography to invasive species and, most recently, contemporary climate change, all involve populations that shift or expand their range over time. Understanding the ecological and evolutionary processes that occur during range shift is of critical importance now that many species are shifting their ranges as a consequence of human-induced climate change (Hill *et al.* 1999; Parmesan & Yohe 2003). Under a changing climate, it is clear that the ability of a species to track climate change by range shift will be a major determinant of extinction risk (Thomas *et al.* 2004).

The rate at which a population spreads through space is a function of the rates of population growth and dispersal (Fisher 1937; Skellam 1951). Indeed, almost all population dynamics can be described by these key population

characteristics coupled with density dependence. Together, these three population characteristics (reproductive rate, density dependence and dispersal) summarize all the organismal traits that allow individuals to disperse, reproduce and survive. Evolution in any life-history trait will result in a change in at least one of a population's three summary characteristics. To avoid confusion between these summary characteristics and the traits behind them, in this study we designate the traits associated with population growth as r^* ; traits associated with density-dependent responses as K^* ; and traits associated with dispersal as D^* .

When species shift their range they encounter a suite of new selection pressures (Suarez & Tsutsui 2008). Some of these arise from encountering a new physical or biotic environment, whereas others are a consequence of the range-shifting dynamics itself. Rapid evolution in response to these selection pressures can affect the population dynamics of range expansion which can, in turn, further feedback on the evolutionary processes (Travis & Dytham 2002; Lambrinos 2004; Burton & Travis 2008a). Rapid

evolution is increasingly observed in nature (Mooney & Cleland 2001; Reznick & Ghalambor 2001) and variation in life-history traits have been observed across dynamic species ranges. For example, recent work on the evolution of dispersal clearly demonstrates selection for increased dispersal on expanding range edges (Travis & Dytham 2002; Hughes *et al.* 2007; Phillips *et al.* 2008). Individuals of greater dispersal ability tend to be the first to arrive at an expanding front and benefit from the lower competitive environment found there (Thomas *et al.* 2001; Hanski *et al.* 2002, 2004; Phillips *et al.* 2006; Hughes *et al.* 2007).

Although the effect of range expansion on the evolution of r^* and K^* remains largely unexplored, classic ecological theory related to r - and K -selection (Roughgarden 1971; Charlesworth 1971) leads us to have clear expectation as to the direction of change. In newly colonized habitats, individuals are r -selected while they tend to K -selected in habitats where populations are long established (Gadgil & Solbrig 1972). So we anticipate that the reduced population density found at an expanding front should drive selection for increased reproductive effort, because in an exponentially growing population (such as that on an expanding front), any small increase in reproductive rate will, over time, result in substantially larger population sizes: classical r -selection (MacArthur & Wilson 1967). In contrast, individuals behind the front are typically in higher density conditions and are therefore expected to be K -selected.

Although the above considerations are likely to hold true for a population expanding into unoccupied space, it is unlikely to be as straightforward when the range expansion is into an area occupied by a competing species. This will most often be the situation, for example, in species shifting their range as climate changes. Indeed, in such a situation, often one species will be expanding its range into that currently occupied by a congener. In the presence of a competitor, we might expect a greater degree of K -selection, reducing the increase in r , thus slowing range expansion. Similarly, the presence of a competitor is likely to have hitherto unexplored consequences for dispersal evolution, particularly if a trade-off exists between investment in D^* and K^* .

To explicitly investigate the possibility of evolved shifts in r^* , K^* and D^* during range expansion, we need a system within which all three can evolve. An important facet of life-history theory is the covariance in the evolution of traits due to trade-offs (Stearns 1989). Although trade-offs have been described within numerous taxa (Roff 2002), there remains relatively little empirical or theoretical understanding of how they evolve and how evolution proceeds once such a trade-off is established (Roff & DeRose 2001; Roff & Fairbairn 2007). Importantly, most evolutionary models usually include only two of our three critical life-history characteristics, and space is considered implicit (Roff 2002).

The first objective of this study was to introduce a novel model where individuals divide a fixed quantity of resource between r^* , K^* and D^* in proportions set by their genotype. In our system, all three critical life-history traits trade-off against each other: increased investment in r^* can evolve, but it comes at a cost to either, or both, K^* and D^* . The second objective was to use the model to establish how the three traits evolve during the range expansion of a species into unoccupied space. The third objective was to determine the robustness of the results obtained in a single species model to the addition of a competing species; for this we simulate the range expansion of one species into a region already occupied by a second species.

METHODS

We extend previous discrete-space modelling approaches (Travis & Dytham 2002; Travis *et al.* 2007; Burton & Travis 2008b) in using an individual-based spatial model to simulate range expansion of asexually reproducing, haploid individuals with discrete generations. We model the evolution of three traits in a population undergoing range expansion. Each individual carries three pseudogenes that determine the proportion of resources allocated to each trait, with equal and non-limiting distribution of resource to all individuals. Each of the three traits [dispersal propensity (D^*), reproductive capability (r^*) and competitive ability (K^*)] is fully heritable with a small probability of mutation.

Spatial population dynamics

Simulations are carried out on a rectangular stepping-stone grid (20 rows \times 15 000 columns) with reflective boundary conditions above the top and below the bottom row and absorbing boundaries at the rear edge of the range. An initial population of individuals is introduced in an area of 20×20 patches at the far left of the arena and left to evolve in a stationary population before being allowed to expand across the remainder of the lattice. Range expansion is initiated once the stationary population has reached evolutionary equilibrium. A population that has reached an equilibrium state is used as the starting point of each simulation as prior evolutionary history can affect the resulting evolutionary pathway of populations undergoing range expansion (Keller & Taylor 2008).

We used a simple population model where individuals reproduce and die, and juveniles compete to attain adulthood. Individuals carry three pseudogenes determining relative allocation to reproduction (pRep), competitive ability (pComp) and dispersal (pDisp). Adults reproduce a number of offspring drawn from a Poisson distribution with mean λ , determined by the maximum possible mean

number of offspring, R and the individual's heritable reproductive allocation (pRep) as follows:

$$\lambda = \text{pRep} \times R$$

Each offspring then disperses with probability pDisp (determined directly from their dispersal trait) to one of the eight nearest neighbouring patches. After dispersal, juvenile competition occurs. A juvenile's survival probability is established from its genotype as a function of the equilibrium density (K) and the sum of the competitive abilities of all individuals (sComp) in the patch as follows:

$$\text{Survival probability} = \min\left(K \times \left(\frac{\text{pComp}}{\text{sComp}}\right), 1\right)$$

Offspring inherit life-history from their parents with a probability of mutation m to each trait. When a mutation occurs, it only occurs to one of the traits. In our simulations, we use values of m of 0.01 and 0.001. The deviation of any subsequently mutated trait from the parental genotype is determined by the magnitude of mutation m_m . For instance, if $m_m = 0.1$ then the difference between the juvenile and adult proportion will be drawn

from a uniform distribution between -0.1 and 0.1 . Where specified we use m_m of 0.1 and 0.3 in our simulations. If the resulting proportion after mutation is negative, then the proportion for that trait is taken to be zero (and if the mutation leads to a proportion greater than 1, it will remain as 1). Any mutation that occurs to one trait (e.g. *Trait1*) will affect the proportion of investment in the other two traits (*Trait2* and *Trait3*). If the magnitude of this mutation is negative then an increase will be observed in *Trait2* and *Trait3* whereas a mutation that results in an increase to *Trait1* will lead to a decrease in *Trait2* and *Trait3*. This allows a trade-off between the three traits to naturally evolve in the simulations. The effect of the mutation on *Trait1* on the proportion of investment in *Trait2* and *Trait3* scales with the current values of *Trait2* and *Trait3*. So if we were to have the proportions allocated to each trait shown in the example below, then the mutation to *Trait1* leads to a greater depletion in *Trait3* than *Trait2*:

where $\textit{Trait1} = 0.2$ $\textit{Trait2} = 0.2$ $\textit{Trait3} = 0.6$
 And mutation to $\textit{Trait1} = 0.1$
 Then $\textit{Trait1} = 0.3$

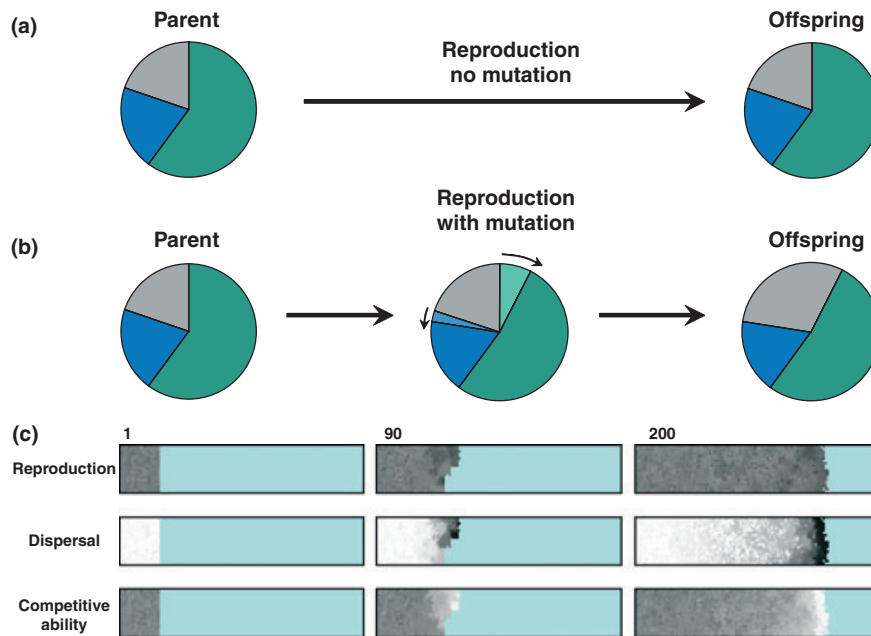


Figure 1 Illustrating key features of the model. (a, b) Pie charts to illustrate the proportion allocation to each trait. Here, an example is shown where *Trait 1* is reproduction, *Trait 2* is dispersal and *Trait 3* is competitive ability. (a) Reproduction occurs without any mutation. (b) A mutation to reproduction occurs with $m_m = 0.1$, as outlined in the Methods section. Here, the parental proportions are shown followed by the shift in proportion and finally the resulting proportions of the offspring. Reproduction is represented by grey, dispersal by blue and competitive ability by green. These values affect the probability of reproduction, dispersal and survival as stated in the Methods section. (c) Snapshots taken from an example simulation 1, 90 and 200 generations after the population is allowed to expand across the grid. For illustrative purposes, only a small portion of the entire range is shown. The grey scale in each picture shows the proportion allocation to reproduction, dispersal and competitive ability respectively. The blue area of the arena depicts unoccupied space. Here, values of $K = 20$, $R = 3$, $m_m = 0.1$ and $m = 0.01$ are used.

$$\begin{aligned} \textit{Trait}2 &= \textit{Trait}2 - \left(\text{mutation} \times \left(\frac{\textit{Trait}2}{\textit{Trait}2 + \textit{Trait}3} \right) \right) \\ &= 0.2 - \left(0.1 \times \left(\frac{0.2}{0.8} \right) \right) \\ &= 0.175 \end{aligned}$$

$$\begin{aligned} \textit{Trait}3 &= \textit{Trait}3 - \left(\text{mutation} \times \left(\frac{\textit{Trait}3}{\textit{Trait}3 + \textit{Trait}2} \right) \right) \\ &= 0.6 - \left(0.1 \times \left(\frac{0.6}{0.8} \right) \right) \\ &= 0.525 \end{aligned}$$

This mutation to *Trait1* is illustrated in Fig. 1a,b, where *Trait1* is reproduction, *Trait2* is dispersal and *Trait3* is competitive ability.

Simulation experiments

The far left of the arena is initially populated with 500 individuals, randomly allocated to an area of 20×20 patches. This population is left to evolve for sufficient time that it reaches a state of equilibrium. Then it is allowed to expand across the lattice (Fig. 1c). Simulations are conducted to answer questions related to the subsequent range expansion, as detailed below.

Change in rate of range expansion

First, we assess the rate of range expansion over 3000 generations. Here, the model is run 20 times for $m = 0.01$, $m_m = 0.1$, $K = 10$ and $R = 3$ and 9. At each time-step, we record the distance between the current population front and the initial starting point. We calculate the rate of range expansion taken as the number of columns moved in 100 time steps.

Evolution of life-history strategies

The next simulations are designed to assess how life-history strategies evolve under range expanding conditions. Following 10 000 generations of range expansion, we collect data on the average proportion allocated to each of the three traits. The large amount of time (10 000 generations) ensures that the traits on the expanding front have evolved to equilibrium, although the rate of range advance stabilizes well before this time (Fig. 2). We record the mean value for each gene from the right-most patch in the range at 10 000 generations and the mean value for each gene in this cell over a subsequent 200 generations. In this way, the mean trait value across every individual in this patch is assessed through time since it is first colonized. We run these

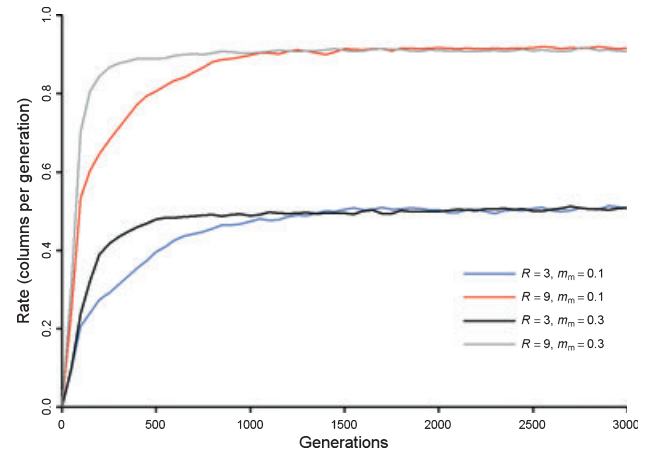


Figure 2 The rate of range expansion through time given as the number of columns moved per generation. Here, the average rate of 20 repetitions of the model is shown for the values of R and m_m .

simulations and calculate the mean of 20 runs using K of 10 and 40, R of 3 and 9, m of 0.01 and 0.001 and m_m of 0.1 and 0.3.

Effect of R and K

A third set of simulations examines the effect of R and K . We run 20 simulations for different combinations of R and K and record the average trait values that evolve at the front and in the stationary range. Here, we use values of K from 5 to 60 in increments of 5 and values of R between 3 and 8 in increments of 1.

Interspecific interactions

We investigate the effect of interspecific interactions on the rate of range expansion and the evolution of traits in the range expanding species by introducing a competitor. For clarity, we refer to the species undergoing range expansion as the invasive species and the species already present within the range as the native species (although this situation could also refer to non-invasives). Regions of the lattice not occupied by the stationary population of the invasive species are fully populated with the native species. In each of the simulations, the carrying capacity applies to the combination of both species, not each species separately, and thus the juveniles of the invasive species have to also compete with individuals of the native species to attain adulthood. In most simulations, native individuals have a fixed competitive ability $Comp_N$, and growth rate R_N . The number of native offspring each generation is taken from a Poisson distribution with mean R_N . Individuals of the native species disperse to one of the nearest eight neighbouring patches with probability 0.1.

Initial simulations are undertaken to assess the rate of range expansion following the same method as used in

Change in rate of range expansion section. We also assess how life-history strategies evolve during range expansion following the methods used in Evolution of life-history strategies section. In both of these instances, we run simulations using m of 0.01, m_m of 0.1, K of 20 and R of 6. We use Comp_N of 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6 and 0.7 and R_N of 1.1, 2, 3, 4 and 5 leading to 40 combinations of Comp_N and R_N . Finally, we run a small set of simulations where both native and introduced species can evolve their relative investments in the three traits. In these simulations, the species play by the same rules in all respects except that the invasive is given a higher R .

RESULTS

Figure 1c illustrates typical dynamics of the simulation model, showing that the proportion of resource allocated to dispersal is greater at the expanding range margin than the stationary population or the core of the moving range. A smaller increase in reproductive allocation at the front is also observed, contrasting with a strongly reduced allocation of resources to competitive ability.

Change in rate of range expansion

Across parameter space, the rate of range expansion typically increases through time (Fig. 2). This acceleration

is highest in the very early stages of range expansion and quickly levels out to an equilibrium rate of range advance (Fig. 2). The acceleration in the rate of expansion is greater when m_m is larger (0.3 compared with 0.1). The equilibrium rate of the range expansion, however, is independent of m_m . Reducing the maximum potential growth rate of the population leads to an overall decrease in the rate of range expansion.

Evolution of life-history strategies

Evolved shifts in life-history are investigated by assessing the mean trait values in a cell on the lattice from initial colonization through 200 generations (Fig. 3). The allocation to dispersal and reproduction is greater at the front than in the core and the difference is typically greater for dispersal than it is for reproduction. In the case of reproduction there is not always a straightforward decline from front to core. Instead, there is often an initial decline just behind the range front followed by a subsequent increase towards the core of the range. Contrastingly, much lower allocations to competitive ability evolve at the front of the range and allocation to this trait increases from the front to the core.

These general results are robust across parameter space: we find qualitatively similar results across all values of R , K and m that we tested. Figure 3 illustrates the quantitative

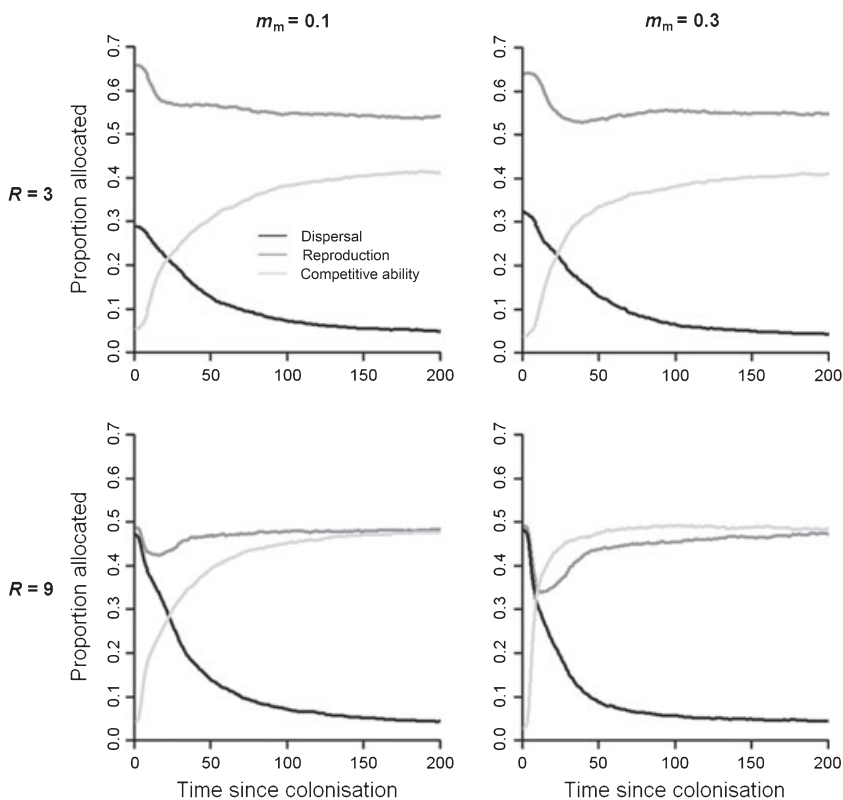


Figure 3 The change in the proportion allocated to each trait from the front of the range through time. We show the proportion allocated to each trait for dispersal, reproduction and competitive ability. All results are for $m = 0.01$ and $K = 10$. Results show differing proportions with m_m and R .

differences that are observed for different R and m_m values. Differences in m_m do not appear to affect the trait values that evolve. They do, however, affect the rate at which trait values return to equilibrium values. This is especially the case for $R = 9$ where there is a larger dip in the proportion allocated to reproduction before this trait increases again through to the core of the range. Figure 3 shows the results for $m = 0.01$ and similar results are found for $m = 0.001$. In all of these simulations, the trait values that evolve in the stationary population are almost identical to those found in the core of the range (cf. Figs 3 and 4).

Effect of R and K

Across all values of R and K , there is consistently higher allocation of resources to dispersal at the front of the expanding range compared with stationary conditions (Fig. 4). On the range edge, the maximum allocation to dispersal is 0.483 compared with a maximum of 0.067 that evolves in the stationary population. The lowest value of dispersal that occurs at the leading edge of the range (0.294) is also much higher than that exhibited in the stationary range (0.001).

Higher investment in reproduction also consistently evolves on the front of an expanding range, although the magnitude of the shift is greatest when R is small and K large. Allocation to reproduction at the expanding front lies between 0.676 and 0.477. These values overlap slightly with the values that evolve in the stationary population (which lie between 0.560 and 0.467).

In contrast to the trends for dispersal and reproduction, there is much lower investment in competitive ability at the front of an expanding range than in a stationary range (Fig. 4). In a stationary population, the resource allocated to competitive ability varies with R and K : ranging between 0.507 and 0.373, but is always much higher than the maximum proportion that evolves at the front of an expanding range (maximum of 0.074).

Varying R and K values led to changes in equilibrium trait values that evolve in both stationary and range expanding populations (Fig. 4). We consider first the trends for a stationary population. Here, extremely low levels of resource are allocated to dispersal; however, there is a slight increase in the allocation to this trait at low K . By contrast, there does not appear to be any variation in dispersal across R . Slightly lower reproductive allocations evolve as K and R are increased, but the opposite is true for competitive ability (where low values of K and R yield much lower resource allocation to this trait). As K increases, the proportion of resource allocated to competitive ability also increases, especially when R is greater than 4. To determine the role of demographic stochasticity in driving this result, we quantified the number of empty patches present within the stationary population. At higher values of K , there is almost no extinction of patches within the stationary population, which contrasts with the situation when low values of K are used. For example, when $K = 5$ the average number of empty patches over the 20 repetitions (just before the population was allowed to expand) was 7.6 and only 0.34 for K of 10 (both for $R = 3$).

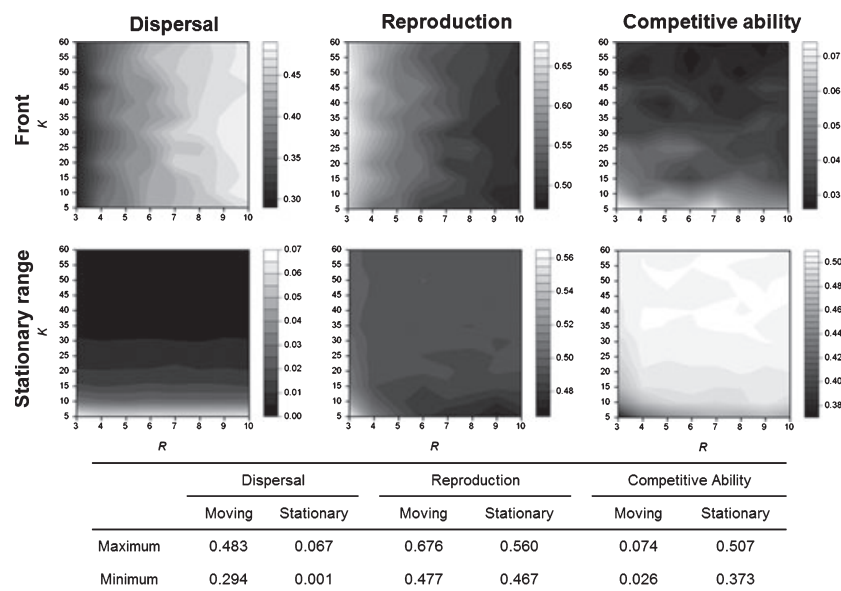


Figure 4 Surfaces showing the mean proportion for each trait for a range of K and R values. We show the results for the front of the range and for the stationary range for dispersal, reproduction and competitive ability respectively. The table shows the maximum and minimum values for each of the contour plots.

Varying R and K has a markedly different effect on the trait values that evolve on the front of the range (Fig. 4). Here, allocation to dispersal increases as R increases and it appears that there is no effect of increasing K (Fig. 4a). The opposite is the case for reproduction, where there is a decrease in allocation to this trait with increasing R . For competitive ability, there is a very small increase in the proportion that evolves at the front of the range at low K and lower values of R .

Interspecific interactions

Although an acceleration in the rate of range expansion of an invasive species is observed when it is in competition with a native species (Fig. 5), the equilibrium rate of range expansion can be substantially reduced compared with that achieved in the absence of a competitor. For example, a species expanding its range into a region occupied by a competitor with high reproductive rate ($R_N = 5$) spreads at only one-eighth the rate of the same species expanding into an empty arena (0.1 columns per generation compared with 0.8). The equilibrium rate of range expansion is determined by the competitive ability ($Comp_N$) and reproductive rate (R_N) of the native; increasing either $Comp_N$ or R_N lowers the rate of expansion. We see qualitatively very similar results across the full range of parameter space investigated.

As $Comp_N$ and R_N are increased, we also see a decrease in the proportion allocated to dispersal at the front of the range compared with that attained when there is no native species present (Fig. 6). This reduction can be substantial. Comparing the same scenarios as above, we observe an increase in dispersal from 0.02 in a core population to 0.42 at an expanding front when there is no competitor, whereas in the presence of a competitor with $R_N = 5$ the investment in dispersal only reaches 0.08 at the front. In turn, we also observe an increase in the proportion allocated to competitive ability and small changes to reproduction. It is worth noting that in all cases where the invasive species survives, there is a higher allocation to dispersal at the front of the range than in the core of the population.

For clarity, on Figs 5 and 6 we have only presented data for values of R_N and $Comp_N$ for which the invasive species always survived. In regions of parameter space where a native species has high competitive ability combined with high reproductive rate the invasive often fails to establish and spread. For some combinations of parameters, it always fails, whereas elsewhere in parameter space it sometimes establishes and spreads.

In simulations where both native and invasive species can evolve their relative investments in the three traits, we obtain results that are consistent with those where only the invasive can evolve. The native species typically suffers rapid local displacement as the invasive spreads and we observe

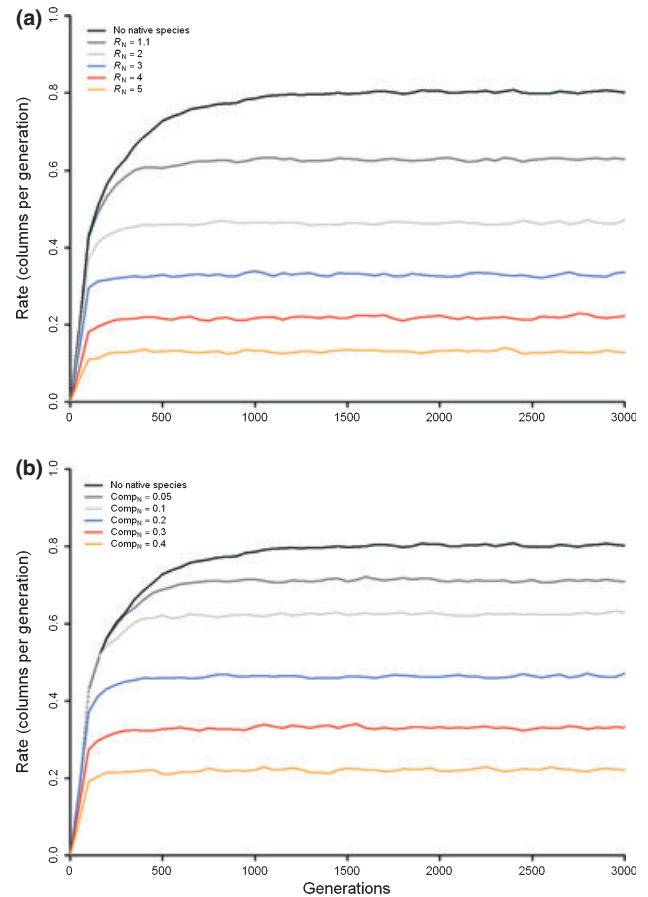


Figure 5 The presence of a native species can substantially reduce the rate at which an invasive species expands its range. The rate is given as the number of columns moved per generation. Here, the average rate of 20 repetitions of the model is shown for (a) $Comp_N$ of 0.2 and (b) R_N of 2. (a) and (b) also show the rate for when there is no native species present.

little or no evidence of evolution of the native's strategy at its retreating range margin.

DISCUSSION

Regardless of their complexity or purpose, population models require parameters that summarize how organisms disperse, reproduce and respond to density effects. The model we present here allows growth rate, relative competitive ability and dispersal propensity to evolve simultaneously as they respond to selection, spatial assortment and the constraints imposed by trade-offs. Our model shows that a population's life-history traits evolve in a consistent manner during range expansion. Periods of range expansion lead to considerably altered investment in traits at the front of the range compared to the core of the population (or in stationary ranges). Specifically, investment in dispersal and

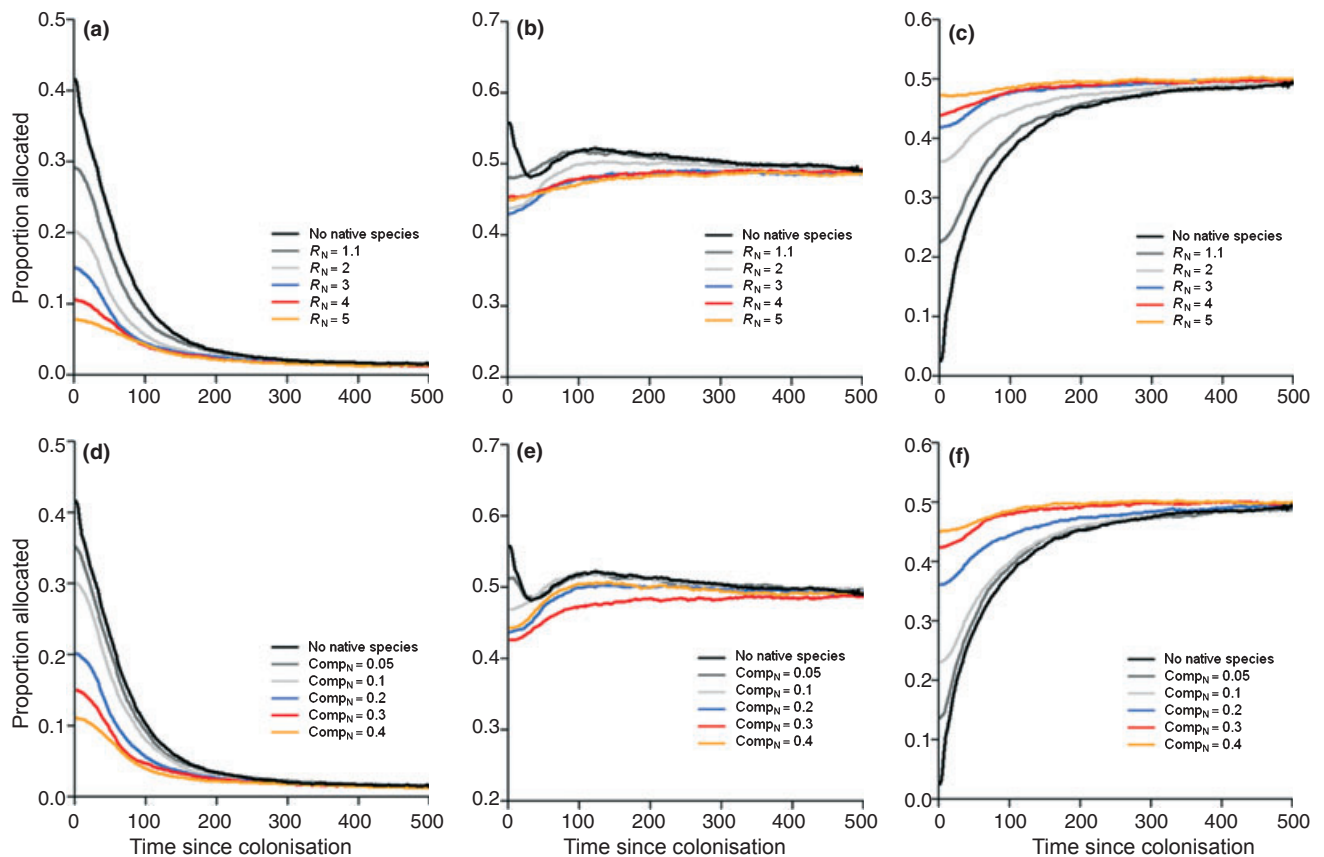


Figure 6 The presence of a native species constrains the degree to which increased investment in dispersal occurs. The change in the proportion allocated to each trait from the front of the range through time. The proportions are shown for dispersal (a) and (d), reproduction (b) and (e) and competitive ability (c) and (f). (a–c) Results for $Comp_N$ of 0.2 and (d–f) R_N of 2. Each graph also shows the proportions allocated when there is no native species present.

reproduction is typically greater at the front of a range expansion whereas investment in competitive ability is lower.

Individuals on the expanding range edge consistently evolve highly dispersive characteristics. This is a well-understood result that is driven by assortment by dispersal ability and lowered density on the expanding population edge (Travis & Dytham 2002; Phillips *et al.* 2008). In our model, as individuals reproduce and mutations occur, the amount of resource allocated to dispersal at the range front increases until an optimal frontal strategy is obtained. In addition to selection for increased dispersal, range expansion also results in a much lower population density at the front of the range than anywhere else in the population. This low population density reduces the requirement for investment in competitive ability and leads to *r*-selection, where a lack of overcrowding in a population selects for increased investment in reproduction (MacArthur & Wilson 1967).

The evolution of higher reproduction and dispersal on the expanding front is at the expense of competitive ability. Away from the front, there is a much greater density of individuals and selection acts to increase investment in competitive ability. Individuals in the range core with a low competitive ability have a much lower chance of surviving to reproductive age and passing on their genes. In the range core, there is also little advantage in dispersing to similarly dense patches, and therefore reproduction and competitive ability evolve at the expense of dispersal.

The equilibrium density (K) determines the optimal allocation between life-history traits in our model. In the core of the range (or in stationary ranges) when equilibrium densities are low, there is increased demographic stochasticity and increased kin competition, both of which typically select for more dispersive individuals (Comins *et al.* 1980; Olivieri *et al.* 1995; Gandon & Michalakis 1999; Poethke *et al.* 2007). Thus, low K leads to slightly higher investment in dispersal in stationary ranges. At the expanding range

front, patches are consistently below equilibrium density, so changes in K do not affect the evolution of life-history traits in this region. The maximum potential growth rate (R) of the population, however, does affect the evolution of traits at the expanding range front (Fig. 4). At the expanding front selection tends to favour increased offspring production and increased dispersal propensity. However, when R is lower, it requires a greater proportional investment in reproduction to produce more offspring. Therefore, a greater allocation to reproduction is required to obtain an optimal balance between reproduction and dispersal.

Theory related to the evolution of dispersal during range expansion has typically ignored the potential role of interspecific interactions (e.g. Travis & Dytham 2002; Phillips *et al.* 2008; Travis *et al.* 2009). In reality, most species undergoing range expansions will encounter interspecific competition. Our results emphasize that the presence and strength of these interactions can substantially modify the dynamics of range expansion. Clearly, the presence of a competitor has an immediate ecological impact; competition reduces the realized growth rate of the invasive species at the front. But the competitor also has an important additional effect through constraining the degree to which a life-history can evolve. The presence of a second species imposes a limit on the extent to which increased dispersal will evolve, where this is at the expense of competitive ability, thus reducing the acceleration in range expansion.

In most of our two-species simulations, we specified a constant life-history for the native. In reality, as an invasive comes into contact with a native it is likely to impose a new selective pressure. However, if the native suffers rapid local displacement by the invasive species, evolution of the native's life-history is unlikely to occur at its retreating range margin. Our initial simulations allowing evolution of the second species confirm this; it is only when the two species are close to competitively neutral that local interactions persist for sufficiently long enough that evolution of life-histories may occur.

Our results serve to emphasize the need for a much greater consideration of interspecific interactions in work seeking to understand and predict the dynamics of range expansion. As work progresses in this direction, it will become increasingly important to incorporate trade-offs between life-history characteristics: if we had modelled the evolution of dispersal assuming no trade-offs with competitive ability or investment in reproduction, we would not have obtained the striking differences in dispersal evolution when a second species was added. Currently, our model better represents the spread of an invasive species into an area already occupied by a native than it does species assemblages shifting their ranges in response to environmental change. Future extensions to the model, incorpo-

rating both gradients in resource availability and allowing local adaptation along an environmental gradient, would potentially yield important new insights into the relative roles of (and interplay between) local adaptation, dispersal evolution and species interactions during periods of climate-induced range-shifting.

Clearly, one important aspect of our model is the trade-off structure. There is good empirical evidence for pairs of life-history traits trading off against each other (Roff 2002): between fecundity and dispersal (Roff 1986; Zera & Denno 1997; Karlsson & Johansson 2008; Saglam *et al.* 2008), competitive ability and reproduction (Strauss *et al.* 2002) and between dispersal and competitive ability (Rodríguez *et al.* 2007). These traits are often labile, evolving rapidly when populations adapt to novel environments (Mooney & Cleland 2001; Reznick & Ghalambor 2001). Newly established and marginal populations have been shown to contain individuals that are more dispersive than in longer established populations (Cwynar & Macdonald 1987; Thomas *et al.* 2001; Hanski *et al.* 2002, 2004; Phillips *et al.* 2006). Additionally, higher growth rates have been found at the front of invasive ranges than in their native range (Davis 2005; Mason *et al.* 2008) or in invaded regions where the species has been long established (Siemann & Rogers 2001; Phillips 2009).

Although there is much empirical support for both the assumptions embedded within our model and its output, some species' responses are not consistent with our model predictions. For example, highly dispersive speckled wood butterflies at range margins reduce investment in reproduction compared with those in the core of the range (Hughes *et al.* 2003). In this species, there is a very strong trade-off between dispersal and fecundity. However, in other butterfly species where the trade-off is weaker, highly dispersive new colonists invest more in reproduction as predicted by our results (Hanski *et al.* 2006). Some initial work, extending the modelling presented here, suggests that dispersal always evolves upwards during range expansion at the expense of competitive ability. However, for these two traits, we find considerable quantitative differences between results depending upon the shape of the trade-offs assumed. Our initial results suggest that whether reproduction increases or decreases during range expansion is dependent upon the shape of the trade-off functions assumed. Thus, if our ultimate aim is to provide predictive models, we require both further development of the modelling and, crucially, empirical work directed towards determining the true shape of functions describing the relationship between individual investment in a trait and the resulting phenotype.

Rapidly accelerating rates of population spread are commonly observed in nature (Shigesada & Kawasaki 1997; Hastings *et al.* 2005). Traditionally, these dynamic spread rates have been explained by careful choice of (static)

dispersal and reproduction parameters (Shigesada & Kawasaki 1997; Clark *et al.* 2001). Our model shows that accelerating range advance can arise, irrespective of the initial dispersal and reproduction parameters, due to life-history evolution. This has implications for both the spread of invasives and those species that are responding to climate change. Although accelerating range advance may be good news for species attempting to track climate change, it is bad news for the management of invasive species.

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