DENSITY-DEPENDENT DISPERSAL AND THE SPEED OF RANGE EXPANSIONS

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ABSTRACT

Aim The speed of range expansions, be it invasive species colonizing a new area or species tracking a moving climatic niche, critically depends on dispersal. Models for species' range expansions generally assume dispersal to be independent of local population densities. However, animals often disperse in response to high population size, or alternatively may avoid or leave areas of very low population sizes. We explore whether such density dependence in dispersal can safely be ignored when predicting the speed of range expansions.

Location Simulation study

Methods We use simulations to examine the effect of different forms of density dependence in emigration and immigration on the speed of range expansions. For emigration, we consider linear and non-linear forms of positive density dependence, negative density dependence at low population densities, and constant emigration rates. For immigration, we consider options where individuals avoid crowded patches, are attracted to the presence of conspecifics or settle independent of local density.

Results The speed of range expansion was slowest when emigration was strongly positively related to density (higher emigration at higher densities) and when individuals avoided settling in low-density patches. It tended to be fastest under negatively density-dependent emigration (higher emigration at lower densities). These results were consistent across two different life histories and different levels of carrying capacity.

Main conclusions Our results suggest that considering density-dependent dispersal and the mechanisms leading to it are important for correctly predicting species' rates of spread. Organisms with a tendency to aggregate, e.g. by relying on conspecific attraction in settlement and emigrating mainly in response to high local densities, are predicted to be least likely to expand their ranges and most at risk from spatial shifts in their climatic niches.

Keywords: Allee effect, climate change, density-dependent emigration, density-dependent immigration, global change, invasion, range expansion, settlement, simulation model

INTRODUCTION

Understanding species' range dynamics under climate change is an urgent goal in conservation biology (Huntley *et al.*, 2010), yet the speed at which species can track a moving climatic niche remains one of the big open questions. Studies of the spread of invasive species suggest that dispersal is the most critical determinant of the speed at which species expand (Neubert & Caswell 2000). Even though species distribution models have started to consider dispersal explicitly (Midgley *et al.*, 2006), it is not yet clear what aspects of dispersal need to be considered. One potentially important aspect of dispersal is its relationship to local population density.

Several local processes can cause the emigration rates from a local patch to depend on density in different ways (Sutherland *et al.*, 2002). Territorial individuals can settle according to the ideal free distribution (Fretwell & Lucas Jr, 1970), where fitness decreases with local density and individuals choose to settle in the patch where they can maximise their fitness. This mechanism leads to positively density-dependent emigration, i.e. higher emigration rates as population densities increase. The relationship between emigration rate and density is expected to depend on the relative quality of the other nearby habitat patches. If territorial individuals settle according to an ideal despotic distribution, where individuals can defend territories (Fretwell & Lucas Jr, 1970), emigration should be related to density in a fashion that resembles a step-wise function. There would be little emigration as long as vacant territories exist in the current cell and full emigration otherwise. Other forms of competition should also lead to positively density-dependent emigration. On the other hand, negatively density-dependent emigration, i.e. increased emigration rates as local density declines, has mostly been related to social factors, for example if aggregations are beneficial for foraging or predator avoidance. If dispersal through areas of high density is risky due to conspecific aggression or high predator presence, negatively density-dependent emigration can also result (Matthysen, 2005). Finally, if individuals disperse due to intrinsic (e.g. genetic or morphological) reasons, emigration rates may be unrelated to density.

Immigration is often density dependent for similar reasons to emigration. It may be more difficult to find a vacant territory in an area of high density, in which case immigration would be negatively density dependent, i.e. individuals are less likely to immigrate into patches of high density. On the other hand, positive density dependence in immigration may arise from conspecific attraction (Stamps, 1988, 2001; Greene & Stamps, 2001). High population densities may indicate good habitat or opportunities for finding a mate. Bark beetles, for example, are strongly attracted to conspecifics (Wood, 1982).

Most theoretical studies assume dispersal rates to be independent of local population density (but see Veit & Lewis 1996). However, if characteristics of dispersal are allowed to evolve, positive density dependence often emerges (Travis, 1999; Kun & Scheuring, 2006; Hovestadt *et al.*, 2010). Positive density dependence was also assumed in the original formulation of source-sink models (Pulliam, 1988). On the other hand, McPeek and Holt (1992) found that optimal dispersal strategies should vary spatially in a way that patches exchange equal numbers of dispersers, thus leading to a negative correlation between local carrying capacity and emigration rate across space. Empirical support for these different forms of dispersal, including negative density dependence, has been found (e.g. Doncaster *et al.* 1997; Diffendorfer 1998; Kuussaari *et al.* 1998; reviews: Denno & Peterson 1995; Sutherland, Gill, & Norris 2002; Matthysen 2005).

Best at al. (2007) recently found that positive density dependence in dispersal can slow species' spatial response to climatic change compared to species with density-independent dispersal. Here, we extend these results by examining a wide range of plausible dispersal forms in terms of their effect on species' range expansion rates in a simulation model. We consider positive and negative density dependence both in emigration and immigration. We limit our investigations to animals that have a distinct dispersive life stage and remain relatively sedentary throughout the rest of their life. We consider two general life histories, an annual life cycle with high fecundity and low survival (e.g. a univoltine butterfly), and a multi-annual life cycle with relatively low fecundity, high survival and overlapping generations (e.g. a non-passerine bird or a mammal).

We distinguish between three phases of dispersal: emigration; transit; and immigration (*sensu* Ims & Yoccoz 1997). We consider density dependence in emigration and immigration, i.e. the decisions to leave and to settle. The distance travelled (transit) has also been found to be density dependent but this may often be a result of density-dependent settlement decisions mostly affecting short movements. The studies that found density-dependent dispersal distances were conducted at relatively small spatial scales (Matthysen, 2005). We do not examine density dependence in dispersal distance explicitly, but it is an emergent property of dispersal subject to density-dependent emigration and immigration.

Species often colonise suitable habitat, e.g. by invading novel areas or because they are lagging behind a spatially moving environmental niche (Kasparek, 1996; Devictor *et al.*, 2008). In these cases, density dependence in dispersal is likely to affect the rate of emigration from habitat patches at the periphery of a species' range where populations will typically be below carrying capacity. If dispersal is positively density dependent, emigration from these patches would be reduced until densities build up to a level where individuals start emigrating. The converse would be true for negatively density-dependent emigration, where a high proportion of individuals would leave these low-density patches until the populations nevertheless build up and emigration rates tended towards values typical for the species. Since dispersal is critical for the spread of species (Kot *et al.*, 1996), we expect the mean emigration rate from local habitat patches to be the main mechanism by which density-dependent dispersal could affect the speed of range expansions. The speed at which recently established marginal populations grow towards high densities, determined by the intrinsic rate of increase (*r*) and carrying capacity (*K*), should also be critical for how density-dependent dispersal affects the speed of range expansions.

METHODS / THE MODEL

We used the spatially explicit, grid based model MIGRATE, which has been described and tested in detail elsewhere (Collingham et al., 1996; Collingham & Huntley, 2000; Hill et al., 2001), to simulate the spatial dynamics of a population across a grid. Local population dynamics within each cell are determined by the life-history of the species. At each time step, a proportion of offspring emigrates and arrives in cells at distances with probabilities that decrease with increasing distance from the source cell according to a bivariate normal distribution. The actual number of offspring which settle in a cell is determined by the amount of available space. So given a positive population growth rate, local populations will grow with a logistic growth rate until the carrying capacity is reached. If a cell receives a fraction p of an individual, it is set to one with probability p and to zero otherwise, thus introducing stochasticity into the model. The simulated species are reproducing sexually and we therefore assume that local populations need at least one female and one male to be established successfully. Assuming an equal sex ratio and no sex differences in dispersal, the probability of an empty cell being colonised by a group of either males or females only is $p_c = \frac{2}{2^n}$ where n is the number of individuals arriving at an empty cell. Newly colonised cells thus get established with probability 1-p_c in our simulations.

We assumed a grid of 500 × 1300 cells of uniform habitat suitability (fixed carrying capacity, *K*). The size of the grid was chosen so as to be sufficiently large to ensure that space did not become limiting in any scenario. Beyond that, the size of the grid had no effect on our results. A block of 10 × 10 cells at the centre of one end along the shorter dimension was populated with 5 individuals per cell at generation 1. After 50 generations, we measured how far along the longer dimension the population had spread, by recording the furthest colonized grid cell.

We examined density-dependent dispersal in three groups of scenarios. First, we varied the shape of the density-dependence of emigration and kept immigration density independent. Then we varied the shape of the density-dependence of immigration while keeping emigration density independent. Finally we varied both, exploring two possible combinations representing species that either avoid areas of high or of low density. See Table 1 for an overview. The forms of emigration rates we examine can be described by the following equation (adapted from Best *et al.* 2007):

$$\varepsilon_t = \varepsilon_K \left(\frac{N_t}{K} \right)^{\gamma} \qquad \text{eq. 1}$$

Here, the emigration rate at time t, ε_t, is a function of the current population size N_t relative to the carrying capacity K. ε_K is the emigration rate at $N_t = K$, and we set it at 0.10. γ determines the shape of density dependence. In our simulations, we used the following values for γ: -0.15, 0, 0.2, 1 and 10 (Fig. 1). γ= -0.15 leads to negatively density-dependent emigration. With γ=0, emigration is independent of density, γ=0.2 describes a concave relationship, γ=1 a linear relationship and γ>1 a convex relationship between emigration and density (Fig. 1). For high values of γ (i.e. 10), emigration approximates a step function with little dispersal for $N_t < K$, but maximum dispersal for $N_t = K$. We chose these scenarios so that they all produced the same emigration rate at carrying capacity. Thus, effects of density-dependent emigration on the speed of range expansion can only be caused by different emigration rates from cells along the range front where carrying capacity has not yet been reached and will not be confounded by different dispersal rates from the saturated core area. The distribution of dispersal distances was density independent and followed a bivariate normal distribution with standard deviation = 50 grid cells. All directions were equally likely.

Using the density-independent emigration scenario, we then considered two different scenarios for density-dependent immigration. In the first scenario, individuals avoid cells with high population density (negatively density-dependent immigration) whereas in the second scenario they avoid cells with low population densities (positively density-dependent immigration). We envision individuals to reach a target cell, but then being able to settle either in the target cell, or one of the eight surrounding cells according to local population density within each of these nine cells. Under the first scenario, individuals leave their target cell if it is at a density higher than 0.7 × K and instead settle in the neighbouring cell with the lowest density among those with densities < 0.7 × K. In the second scenario, they leave the target cell if its density is below 0.3 × K and instead settle in the neighbouring cells with density above 0.3 × K, starting with the one with the highest density but still with available space. All 8 neighbouring cells are examined in order of their perceived suitability according to these settlement rules until all the dispersing individuals have been accounted for or all of the 8 neighbouring cells examined. We used the density of residents in the previous time step as a measure of local population density rather than the number of queuing recruits at the present time step. Since most offspring settle locally under the chosen parameter values, the two densities were nearly identical, but using density of residents greatly reduced the computational burden. Mortality was based on current densities so that K was not exceeded.

Finally, we examined possible interactions between density effects on emigration and immigration in two further scenarios. The first represents a species that avoids high density both when deciding to leave and when deciding to settle. For this scenario, we combined positively density-dependent emigration, assuming $\gamma = 1$, and negatively density-dependent immigration, as described in the previous paragraph. The second scenario represents a species that avoids areas of low conspecific density. We assumed $\gamma = -0.15$ and positively density-dependent immigration.

In total, we therefore had nine scenarios for density-dependent dispersal: five scenarios of density-dependent emigration (Table 1, Fig. 1) with density-independent settlement; two scenarios of density-dependent immigration with density-independent emigration; and two scenarios where both emigration and settlement were density dependent. As a sensitivity analysis to test the effect of the choice of particular parameter values on our results, we ran each of these scenarios at three levels of *K*, crossed by three levels of maximum population growth, *r*, and two life histories, as detailed below. This led to 162 different parameter combinations, each of which we replicated 5 times.

We considered two contrasting life histories to model local population dynamics, which, in the absence of dispersal, follows the general population model

$$n_{t+1} = An_t \qquad \text{eq. 2}$$

where n_t is a vector holding the number of individuals in each stage at time t and A is a population projection matrix. The first life history we consider is an annual organism with

$$A = rs_{annual} \qquad \text{eq. 3}$$

which produces r = 50 offspring that survive to the next step with probability s_{annual}. The algorithm then determines how many individuals emigrate, depending on the dispersal scenarios detailed above, and spreads them across the grid where local population sizes are updated.

The second life-history we consider represents an organism with a multi-year life cycle with

$$A = \begin{pmatrix} 0 & 0 & rs \\ s_{perennial} & 0 & 0 \\ 0 & s & s \end{pmatrix} \qquad \text{eq. 4}$$

It produces r = 4 offspring which survive to the 1st cohort class (1 yr olds) with probability $s_{perennial}$, and thereafter survive with probability s = 0.9. In this life history pairs are needed for breeding. If the number of adults in a cell is ≤ 20 then the number of breeding pairs is drawn from a binomial distribution with sample size equal to the number of adults and probability equal to 0.5, otherwise it is simply assumed to be half the number of adults. This part of the model is another source of stochasticity. Movement happens during the juvenile stage only for organisms with a multi-year life cycle and new recruits to a local cell compete for available space so that the total number of individuals could not exceed K. Movement into one of the eight neighbouring cells may also occur depending on the settlement rules for that particular simulation or if the local cell is full. We envision the first life history to represent an annual insect, such as a univoltine butterfly (e.g. Hill *et al.* 2001), and refer to it below as a butterfly. The second life history could represent a sub-tropical non-passerine bird (e.g. a hadeda ibis, *Bostrychia hagedash*, Duckworth *et al.*, 2012), but the two life histories could apply to many similar species; for convenience we refer to this life history as a bird.

We ran all simulations for three values each of *K* (222, 133 and 44 individuals per cell) and *r*. We manipulated the latter by changing S_{annual} (0.022, 0.025 and 0.028) and $S_{perennial}$ (0.15, 0.34 and 0.6), leading to maximum population growth rates of 1.1, 1.25 and 1.4 for both life histories. By choosing life histories with similar maximum growth rates, carrying capacities and dispersal capabilities, we investigate possible interactions between density-dependent dispersal and life-histories *per se* on the speed of range expansion. We do not necessarily imply that the two life histories are similar in the maximum densities they can reach or the distances they can travel. We imply, however, that the densities and distances are comparable among the two life histories relative to the grid cell size, which we assume can be chosen accordingly.

We examined how the nine scenarios, three levels of *r*, three levels of *K* and two life histories affected the speed of range expansion using a regression tree model (Breiman *et al.*, 1984) implemented in package 'tree' in program R 2.15.0 (Ripley, 2010; R Development Core Team, 2012). A regression tree recursively partitions the response variable (speed of range expansion in our case) into subsets according to its relationship to the factors we varied (density dependence in dispersal, *r*, *K* and the life history). It first splits the data into two groups that are most different, and then each group is further split until homogeneous groups remain. The lengths of the branches are proportional to the reduction in deviance that each split achieves. The main splits and branch lengths therefore visualize which factors or factor levels had the largest effect on the speed of range expansion in our simulations.

RESULTS

Density-dependent dispersal had clear effects on the speed of range expansion (Fig. 2, summary in Table 1). At medium levels of carrying capacity (K) and population growth rate (r), three density-dependent dispersal scenarios strongly reduced the speed of range expansion compared to the density-independent scenario ($\gamma = 0$, Fig. 2, central panel): strongly density-dependent emigration (γ=10), and the two scenarios with positively density-dependent immigration (positively density dependent immigration, PsI, and 'avoid low density', ALD). Weaker positively density-dependent emigration (either alone, $\gamma = 1$, or in combination with density-dependent immigration, AHD) led to a smaller decrease in the speed of range expansion. Negatively density-dependent or weakly positively density-dependent emigration ($\gamma = -0.15$ and $\gamma = 0.2$) had little effect on the speed of range expansion. This general pattern was qualitatively consistent across the two life histories and levels of carrying capacity (K) and intrinsic growth rate (r, remaining panels in Fig. 2).

The effect of density-dependent emigration on the speed of range expansion was mediated by the mean emigration rate at the range edge (Figs. S1 and S2 in the Supplementary Information). The emigration rate increased nearly linearly from the scenario with negatively density-dependent emigration ($\gamma = -0.15$) through to strongly positively density-dependent emigration ($\gamma = 10$).

Above, we presented the effects of density-dependent dispersal on the change in the speed of range expansion compared to the scenario with density-independent dispersal. However, varying density dependence in dispersal, *r*, *K* and the life history all affected the absolute speed at which the ranges expanded. We used a regression tree model to visualize the relative importance of varying these factors on the speed of range expansion (Fig. 3). We pruned the tree to 5 terminal nodes, which yielded a model that explained 87% of the total deviance in our response and clearly shows the most important splits. The first split was between simulations that used a low intrinsic growth rate, *r*, and the rest. With low *r*, range expansion was generally the slowest. The next split in both remaining subsets involved dispersal scenarios, with the 'avoid low density', positively density-dependent immigration and positively density-dependent emigration with $\gamma=10$ leading to slower range expansions than the other dispersal scenarios. The remaining split distinguished between the two life histories (the bird expanded more slowly than the butterfly under the remaining dispersal scenarios and medium/high *r*).

DISCUSSION

Individuals of mobile organisms leave their natal patch to avoid low resource levels, inbreeding or parasites, and tend to settle in places where their fitness prospects are good (Clobert *et al.*, 2009). These processes are likely to lead to emigration and immigration probabilities that depend on local population density (Travis, 1999). We used a simulation model to examine the effect of density-dependent dispersal on the speed at which species' geographic ranges can expand, be they alien invaders or native species undergoing range dynamics.

Density dependence in emigration and settlement had profound effects on the speed of range expansion in our model (see Table 1 for an overview). Range expansion was slowest when emigration was positively density dependent, i.e. where individuals were more likely to emigrate at densities close to the carrying capacity. The reason for this result was that newly colonised grid cells emitted few emigrants until their population sizes had built up. Positively density-dependent emigration is usually found in situations where individuals compete for resources (Sutherland *et al.*, 2002; Matthysen, 2005). Where individuals behave in a manner resembling an ideal-free distribution or ideal despotic distribution (Fretwell & Lucas Jr, 1970), they are only expected to emigrate once local densities in a habitat patch build up; based on our simulations we predict that such species would expand their ranges particularly slowly. Positively density-dependent emigration is expected to evolve under a range of conditions and accordingly to occur frequently in nature (Travis, 1999).

Positively density-dependent immigration, i.e. when individuals avoid settling in patches with low population densities, also led to slow range expansions in our model because individuals emigrating from cells at the edge of the range preferentially dispersed back into cells behind the range front where densities were higher. This type of immigration is a kind of Allee effect (Greene & Stamps, 2001; Courchamp *et al.*, 2008), and can occur when species show conspecific attraction (Doligez *et al.*, 2002). Conspecific attraction affects settlement in many birds (Cam *et al.*, 2004; Serrano *et al.*, 2004; Laiolo & Tella, 2008), insects (Hanski *et al.*, 1994), reptiles (Stamps, 1988) and amphibians (Bee, 2007). Bled *et al.* (2011) found that collared doves (*Streptopelia decaocto*) invading North America colonized new areas in a positively density-dependent fashion. Our results suggest that this trait can reduce the speed with which species can shift their range.

In our model, range expansion tended to be fastest with negatively density-dependent emigration, i.e. where individuals were more likely to leave cells at low population densities, or with density-independent dispersal. This result is consistent with the empirical finding that range expansions accelerate in areas not favoured by a species as individuals move on more readily (Andersen *et al.*, 2004). If this type of emigration is governed by the same behavioural mechanisms as settlement decisions, one would expect negatively density-dependent emigration to be coupled with positively density-dependent immigration. In our simulations, this situation was represented by the scenario 'avoid low density', which led to a greatly reduced speed of range expansion comparable to the scenario with negatively density-dependent emigration alone. Our results thus suggest that understanding the mechanisms that govern decisions to leave or settle in a particular patch are crucially important for predicting how fast a species is able to shift its range.

The two life histories we considered represented two rather different points on the slow – fast continuum (Sæther *et al.*, 1996), with the butterfly representing an annual with high reproductive output and the bird representing a long-lived organism with relatively low reproductive output. We chose both to have the same intrinsic growth rate and carrying capacity. While the butterfly expanded its range more quickly than the bird, both life histories showed the same relationships between density-dependent dispersal and the speed of range expansion. This suggests that our results apply to species across a wide range of life histories.

Our simulations assumed a spatially and temporally constant environment. While environmental heterogeneity would also affect the speed at which ranges change (e.g. Early & Sax, 2011), neither temporal nor spatial heterogeneity should qualitatively change our results. However, species expanding into environments that become slowly more suitable may be close to carrying capacity more often than in the situation we simulated. Since all our scenarios had the same emigration rate at carrying capacity, we would have found smaller effects of density dependence in this situation.

Our simulation model assumes that individuals disperse only once during their lifetime. This is realistic for organisms that have a specific dispersive life stage such as many insects. Even organisms that remain equally mobile throughout their life often have a stage during which they are much more prone to disperse (e.g. juveniles in many birds, Greenwood & Harvey, 1982). For organisms that disperse multiple times, our model is likely to underestimate the importance of density dependence, which could affect dispersal decisions each time an individual decides whether to stay or to leave its patch. Our results are therefore likely conservative.

Under current rates of observed climate change, a big worry is whether species can shift their ranges fast enough to keep pace with a locally changing climate. Our result suggest that organisms that tend to aggregate, for example by relying on conspecific attraction for settlement or by emigrating only in response to high local densities, are most at risk of falling behind a spatially moving climatic niche. Our results also predict that such species would be slower invaders if introduced to new areas. Current modelling approaches are moving towards including more detail on species' demographics and dispersal abilities (Brook *et al.*, 2009; Huntley *et al.*, 2010), and a big question is how much detail needs to be included. Our study demonstrates that density-dependent dispersal can be important for the speed of range expansions, especially if the focal species has a high potential population growth rate.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1 speed of simulated range expansion in relation to mean emigration rate: bird

Figure S2 speed of simulated range expansion in relation to mean emigration rate: butterfly

Biosketch:

Res Altwegg is a population ecologist interested in the effect of climatic and land-use changes on biodiversity. **Yvonne Collingham** is an ecologist interested in species' range shifts under climatic change. **Birgit Erni** is a statistician with interest in ecological applications. **Brian Huntley** is an ecologist, palaeoecologist and biogeographer with broad interests in environmental change and range dynamics.

Author contributions: R.A., Y.C.C. and B.H. conceived the ideas. Y.C.C. developed the simulation model and ran the simulations. R.A. and B.E. analyzed the output. All authors contributed to manuscript preparation.

Table 1. Overview of dispersal scenarios and their effects on the speed of range expansion across a simulated landscape. For the density-dependent emigration scenarios, γ determines the shape of the relationship as plotted in Fig. 1.

	Dispersal scenario	Description	Density effect on	Effect on the speed of range expansion
1	γ = 0	No density dependence in movement	None	Reference scenario
2	γ = -0.15	Negatively density-dependent emigration: higher emigration probabilities from cells at low density	Emigration	Slight increase when r and K were sufficiently high
3	γ = 0.2	Slight positively density-dependent emigration: higher emigration probabilities from cells at high density	Emigration	Slight decrease when K was sufficiently high
4	γ = 1	Moderate positively density-dependent emigration: higher emigration probabilities from cells at high density	Emigration	Clear decrease under most combinations of r and K
5	γ = 10; g10	Strong positively density-dependent emigration: higher emigration probabilities from cells at high density	Emigration	Strong decrease under most combinations of r and K
6	NgI	Negatively density dependent Immigration: higher immigration probability into cells at low density	Immigration	No change
7	PsI	Positively density-dependent Immigration: higher immigration probability into cells at high density	Immigration	Strong decrease in all cases
8	AHD	Avoid High Density: combination of scenarios 4 and 6	Emigration and Immigration	Slight decrease when r and K were sufficiently high
9	ALD	Avoid Low Density: combination of scenarios 2 and 7	Emigration and Immigration	Strong decrease in all cases

Figure 1: Shapes of density dependence that we considered for the emigration rate from local cells to examine the effect of density dependence on the speed of range expansions. See equation 1 in the text.

Figure 2. Change in speed of simulated range expansion achieved under the different dispersal scenarios and two life history scenarios compared to the scenario of no density dependence in movement, as a percentage of the average of the five simulations with $\gamma = 0$. Black symbols indicate significant differences from the density-independent scenario, using Tukey's method for *post-hoc* comparisons. The error bars represent ± one standard deviation, although they are smaller than the symbols in most cases. The vertical dashed lines separate the three groups of scenarios: density-dependent emigration ('$\gamma = -0.15$' … '$\gamma = 10$', see Fig. 1), density-dependent immigration ('NgI' = Immigration negatively density dependent, 'PsI' = Immigration positively density dependent), and both ('AHD' = Avoid High Density, 'ALD' = Avoid Low Density'). The symbols represent the butterfly (filled dots) and bird life history (open triangles), respectively.

Figure 3: Regression tree showing the major factors causing variation in the speed of simulated range expansion. Tree models use predictor variables to split the data into groups in a way that results in the greatest increase in explained deviance. The predictor variables were the nine dispersal scenarios (see Methods section), three levels of intrinsic growth rate (r: 'L', 'M' and 'H'), three levels of carrying capacity (K: 'L', 'M' and 'H') and two life histories ('bird' *versus* 'butterfly'). The text at each node indicates which factor levels were grouped into the left

branch. All others were grouped into the right branch. The numbers at the end of the terminal branches give the mean of the furthest cell reached (our measure of speed of range expansion) across all simulations that were grouped into the branch. (Key to abbreviations: Dispersal scenarios: ‘ALD’ = avoid low density; ‘PsI’ = positively density-dependent Immigration; ‘g10’ = density-dependent emigration with γ=10. Life histories: ‘brd’ = bird.)

Figure 1.

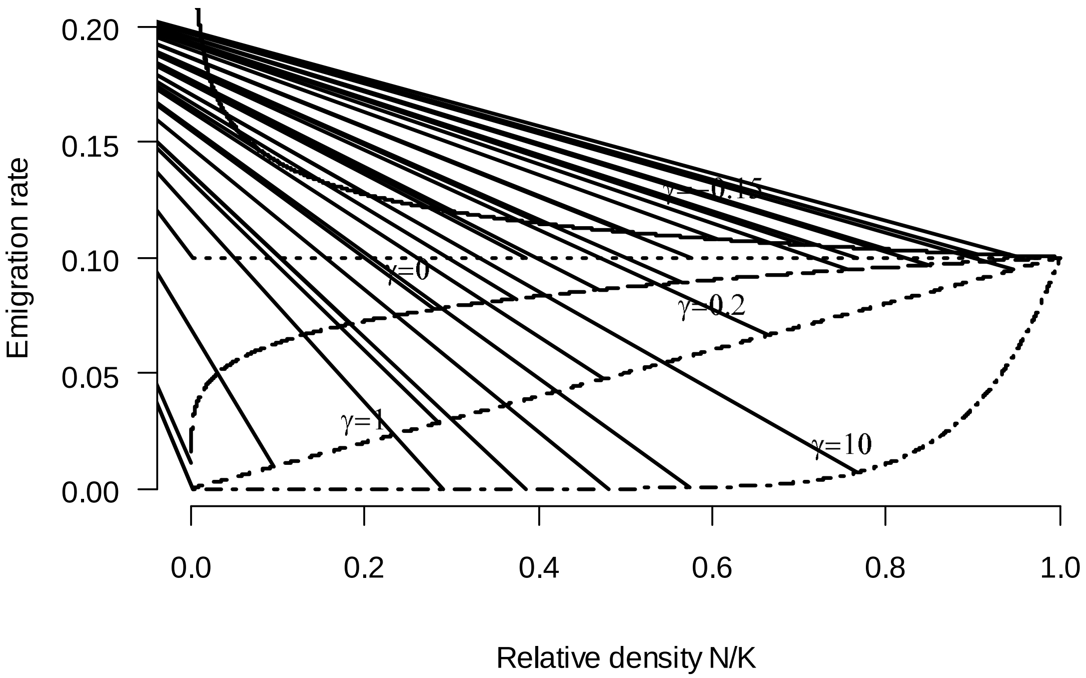

0.20
0.15
0.10
0.05
0.00
Emigration rate
γ=−0.15
γ=0
γ=0.2
γ=1
γ=10
0.0
0.2
0.4
0.6
0.8
1.0
Relative density N/K

Figure 2

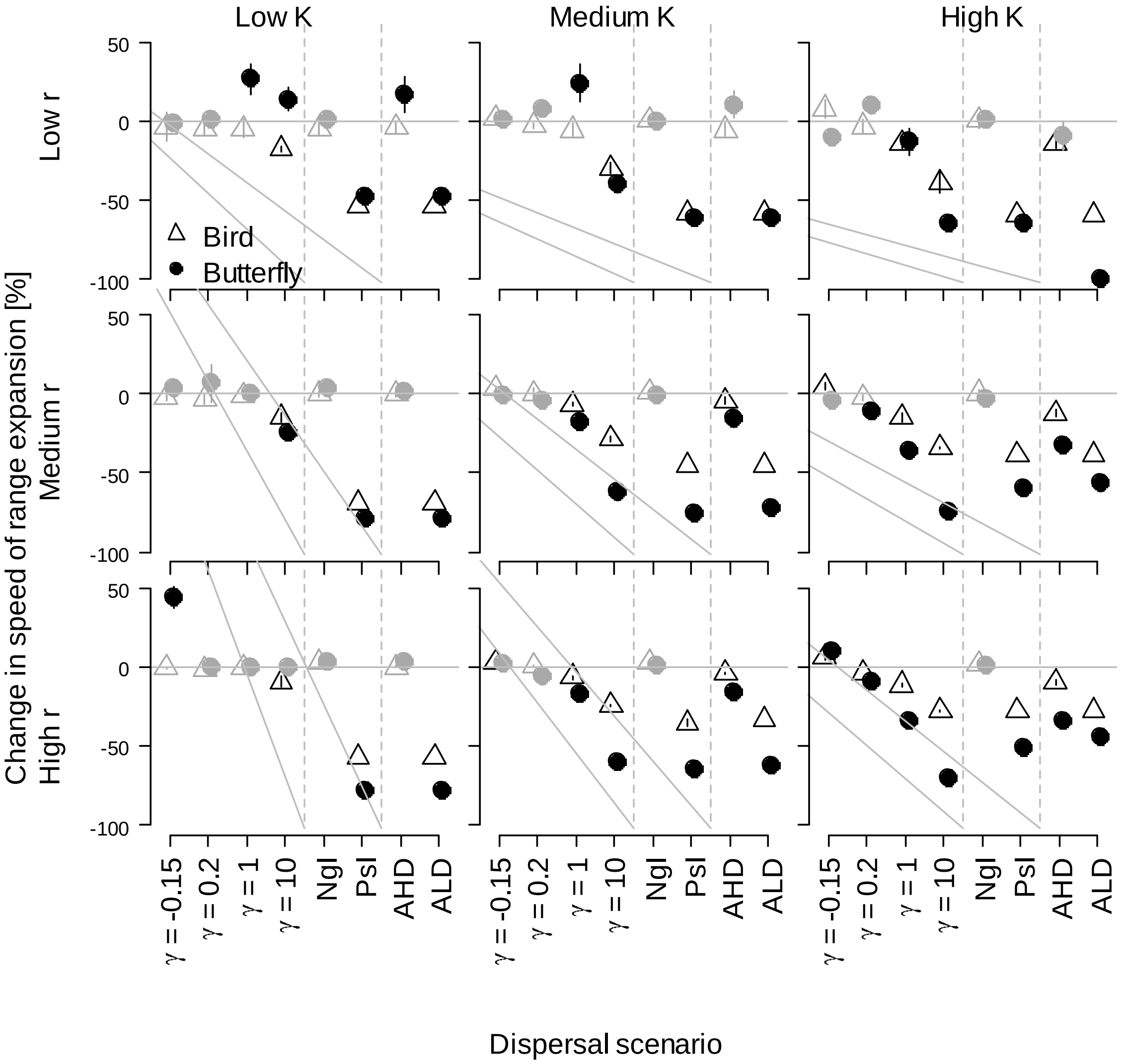
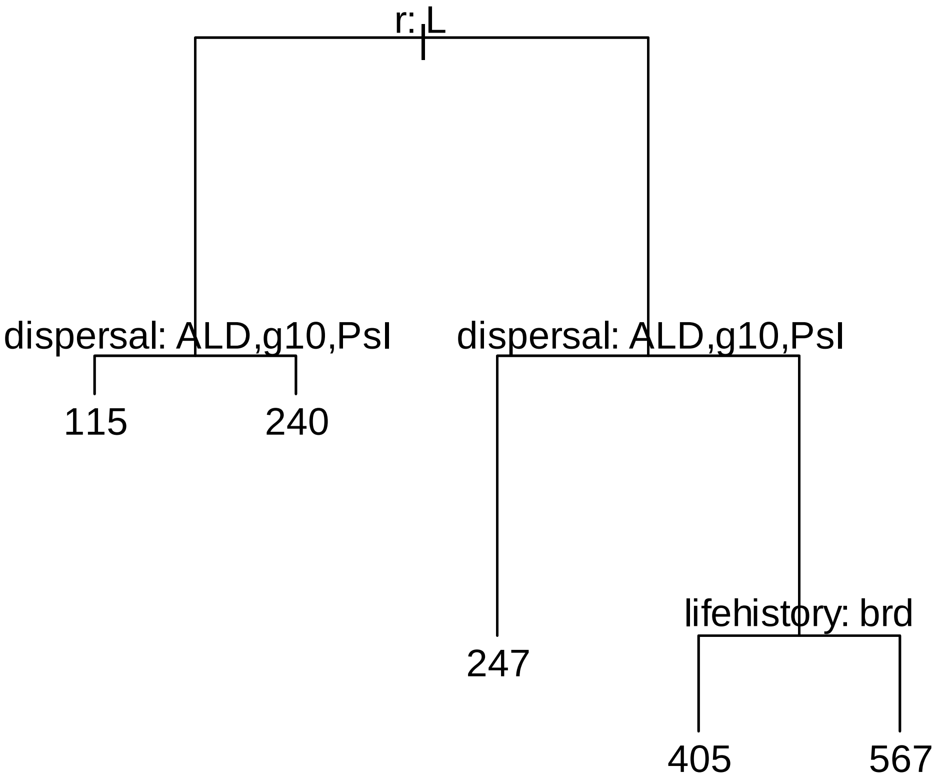

Low K
Medium K
High K
Low r
Medium r
High r
Change in speed of range expansion [%]
50
0
-50
-100
△ Bird
● Butterfly
γ = -0.15
γ = 0.2
γ = 1
γ = 10
NgI
PsI
AHD
ALD
Dispersal scenario

Figure 3


r: L
dispersal: ALD,g10,PsI
dispersal: ALD,g10,PsI
115
240
247
lifehistory: brd
405
567

Supplementary Information

Figure S1. Simulation results for the bird life history (see Methods section for details): speed of simulated range expansion (furthest cell reached on a grid) in relation to mean emigration rate from local cells for nine scenarios that differed in the shape of density-dependent dispersal. Triangles represent the five scenarios of density-dependent emigration illustrated in Fig. 1, using the same colour coding. Squares are two scenarios of density-dependent settlement with density-independent emigration ($\gamma = 0$): more likely to settle in less crowded cells (negative density dependence; orange symbol); and more likely to settle in more crowded cells (positive density dependence; blue symbol). Two scenarios combining density-dependent emigration and settlement are symbolised by '+': orange for a scenario that avoids high density (combining positive density dependence in emigration [$\gamma = 1$] and negatively density-dependent settlement); and blue for a scenario that avoids low density (combining negatively density-dependent emigration [$\gamma = -0.15$] and positively density-dependent settlement).

Figure S2: Simulation results for the butterfly life history: speed of simulated range expansion (furthest cell reached on a grid) in relation to mean emigration rate from local cells for nine scenarios that differed in the shape of density-dependent dispersal. See legend to Fig. 2 for details of the nine scenarios.

Figure S1.

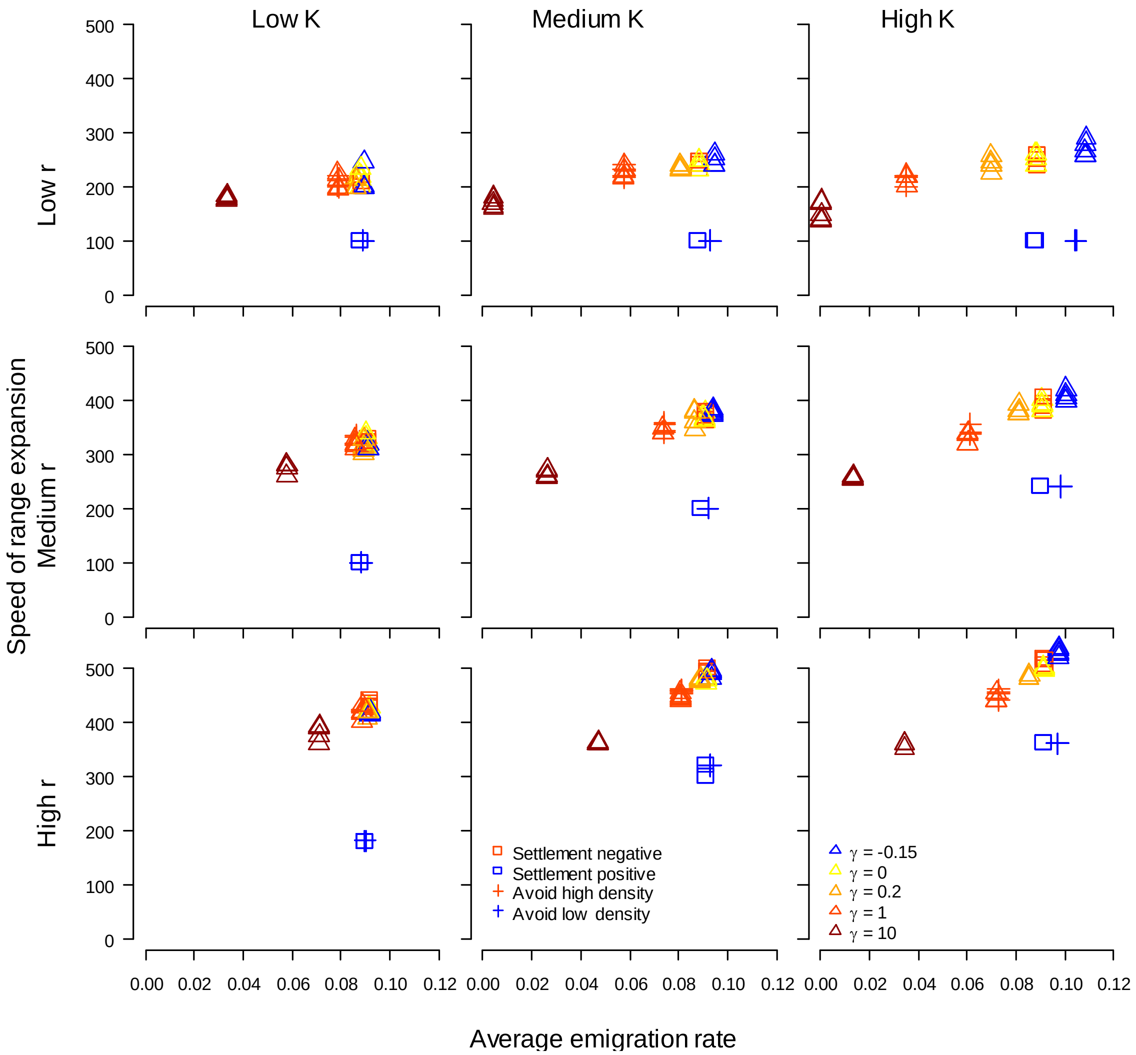
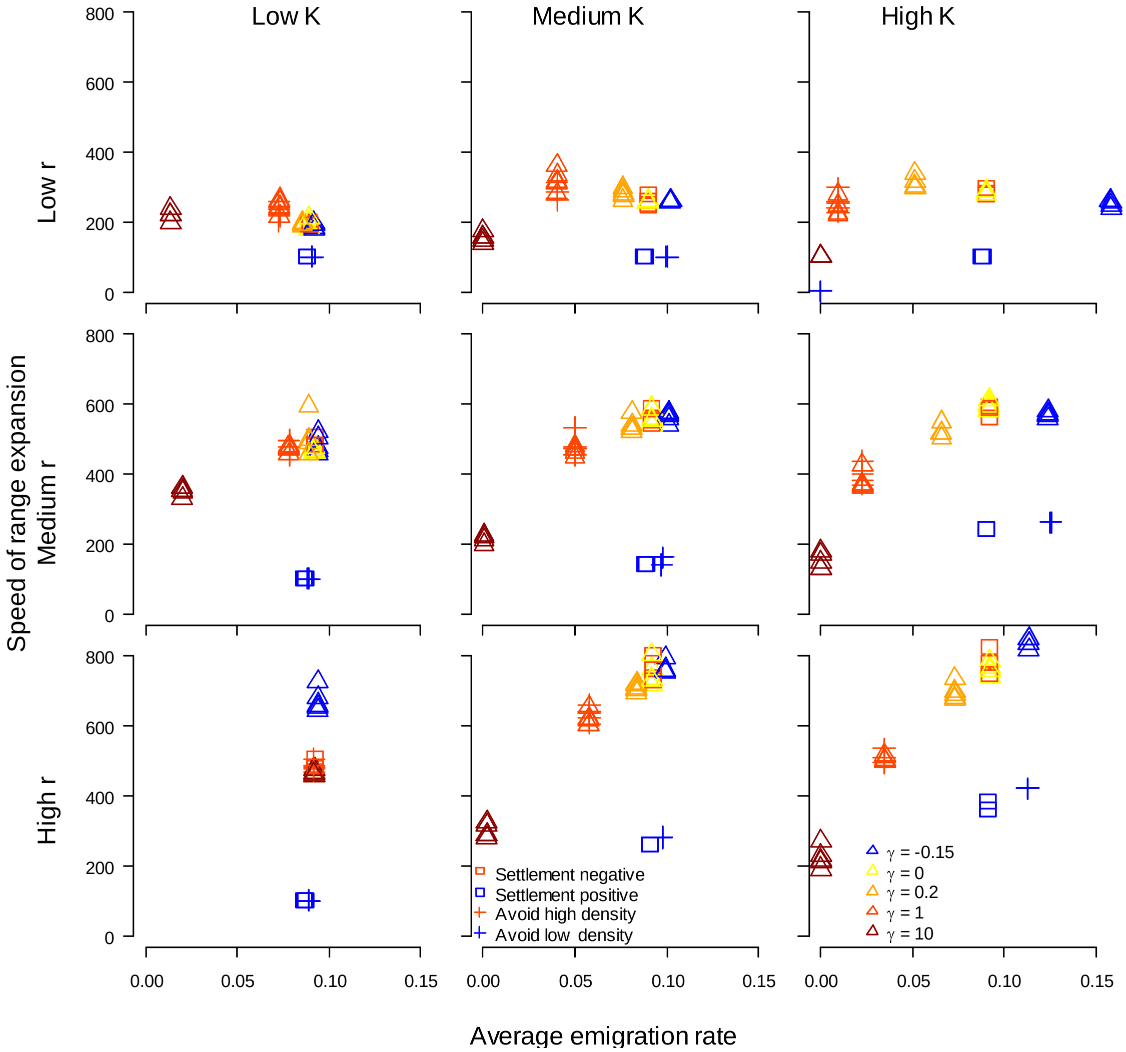

Low K
Medium K
High K
Low r
Medium r
High r
Speed of range expansion
Average emigration rate
0
100
200
300
400
500
0.00
0.02
0.04
0.06
0.08
0.10
0.12
□ Settlement negative
□ Settlement positive
+ Avoid high density
+ Avoid low density
△ γ = -0.15
△ γ = 0
△ γ = 0.2
△ γ = 1
△ γ = 10

Figure S2.


Low K
Medium K
High K
Low r
Medium r
High r
Speed of range expansion
Average emigration rate
0
200
400
600
800
0.00
0.05
0.10
0.15
□ Settlement negative
□ Settlement positive
+ Avoid high density
+ Avoid low density
△ γ = -0.15
△ γ = 0
△ γ = 0.2
△ γ = 1
△ γ = 10