

On the elasticity of range limits during periods of expansion

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Abstract. Dispersal is known to play a crucial role in the formation of species' ranges. Recent studies demonstrate that dispersiveness increases rapidly during the range expansion of species due to a fitness increase for dispersers at the expanding front. R. D. Holt concluded, however, that emigration should decline after the period of invasion and hence predicted some range contraction following the initial expansion phase. In this study, we evaluate this hypothesis using a spatially explicit individual-based model of populations distributed along environmental gradients. In our experiments we allow the species to spread along a gradient of declining conditions. Results show that range contraction did emerge in a gradient of dispersal mortality, caused by the rapid increase in emigration probability during invasion and selection disfavoring dispersal, once a stable range is formed. However, gradients in growth rate, local extinction rate, and patch capacity did not lead to a noticeable contraction of the range. We conclude, that the phenomenon of range contraction may emerge, but only under conditions that select for a reduction in dispersal at the range edge in comparison to the core region once the expansion period is over.

Key words: dispersal; environmental gradients; individual-based model; invasion; range contraction; spatial ecology; species' ranges.

INTRODUCTION

The establishment of species' range borders is the focus of many evolutionary and ecological analyses (Holt et al. 2005, Thomas et al. 2006, Dytham 2009, Gastner et al. 2009, Gaston 2009). Demographic processes at a range margin play an especially important role for understanding range formation and predicting a species future distribution (Holt et al. 2005). As dispersal shapes demographic patterns of populations it plays a key role for the formation of geographic ranges (Bridle and Vines 2007, Gaston 2009).

A well-established observation during periods of range expansion is an increase in dispersiveness (Thomas et al. 2001, Simmons and Thomas 2004, Duckworth 2008, Phillips et al. 2008). This phenomenon is caused by a kind of ecological filter at the front of the travelling wave: more dispersive individuals from the most forward populations are more likely to be found in newly established habitat patches than less dispersive ones. This effect can multiply over generations as emigrants from these patches are most likely to expand

the range even further (Travis and Dytham 2002). Hence, the distribution of genotypes in newly colonized patches is shifted toward a higher emigration tendency. The evolution of emigration at range borders has, however, not received much attention from the side of theoreticians and ecological modelers (but see Gros et al. 2006, Dytham 2009). In a review of MacArthur's (1972) pioneering book about geographical ecology, Holt (2003) concluded that, in stable source-sink systems, dispersal should be selectively disadvantageous, as a consequence of the potential fitness loss of individuals migrating mainly from source to sink populations. He argued that in such systems the source populations will have a population density less than one because of the outflow of emigrants and hence future fitness expectations for philopatric inhabitants are higher. As individuals in sink populations have a lower fitness and more dispersers emigrate from source patches than from sink habitats, the majority of migrants will move downwards in a fitness gradient. This leads to strong selection against emigration. Holt thus concluded that a species' range could shrink after the initial expansion due to selection disfavoring dispersal once (all) new suitable habitats have been colonized.

Manuscript received 29 October 2009; accepted 1 February 2010. Corresponding Editor: A. M. de Roos.

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In most theoretical studies, the authors do not distinguish between the effects of different types of gradients for range expansion and specifically the relevance of Holt's prediction. Gradients modeled either affected reproduction (Travis et al. 2005, Brooker et al. 2007, Rowell 2009), patch size (Bahn et al. 2006), or the individuals' survival probability (Antonovics et al. 2006, Armsworth and Roughgarden 2008). However, in a recent study, Dytham (2009) systematically explored selection on dispersal distance along a variety of gradient types, e.g., in growth and death rate, distance dependent dispersal costs and patch size, with a focus on equilibrium conditions. He showed that the emergent dispersal distances at range margins strongly depend on the conditions that lead to the formation of the species' ranges. Scenarios, in which the spatiotemporal variance increases along the gradient, e.g., reduction in patch size or increased habitat turnover, lead to the evolution of longer dispersal distances in the range border zone than in the core area. In contrast, a gradient in dispersal costs favors lower dispersiveness at the margin than in the core. However, Dytham did not investigate the phenomenon predicted by Holt, i.e., the shrinking of ranges after initial expansion caused by selection for reduced dispersal at range margins. We expect to observe such 'elastic range boundaries' mostly in gradients, where the benefits of dispersal are distinctly larger during expansion than after establishment. These should be gradients that do not greatly affect the variance and/or extinction probability of populations once they are established. This should especially hold for a gradient in dispersal mortality (e.g., habitat fragmentation). In contrast, conditions favoring high dispersal in the margin should not lead to a decrease in emigration probability at the stable range margin and hence we expect no or just slight elasticity of the range border for these cases.

In this study, we thus more thoroughly address the conditions under which range contraction (after initial expansion) might be observed. To investigate the phenomenon we perform individual-based simulations of a spatially explicit metapopulation along four kinds of environmental gradients: (1) declining patch capacity (e.g., patch size), (2) declining per capita growth rate (e.g., patch quality), (3) increasing dispersal mortality (e.g., habitat fragmentation), and (4) increasing probability of externally enforced local extinction (e.g., environmental catastrophes).

THE MODEL

The individual-based simulations we use are applicable to annual organisms with discrete reproduction phases. Similar population models were used, e.g., by Travis et al. (1999), Gros et al. (2006), or Kun and Scheuring (2006). The simulated world is a rectangular lattice, consisting of 100 stripes (*x*-dimension) of 50 patches each (*y*-dimension), i.e., a total of 5000 habitat

patches. Every patch is characterized by specific environmental conditions affecting reproduction, habitat quality, and inter-patch dispersal mortality. Each individual is characterized by its sex, its affiliation with a specific patch (*i*), and by two alleles at one locus that determine the density-independent probability to emigrate. We assume discrete generations. Once in its life, before mating and reproduction, every individual has the opportunity to disperse. Local population dynamics are density-dependent according to the discrete time model developed by Hassell (1975). Every female gives, after mating with one randomly chosen male in the same patch, birth to Λ offspring, where Λ is a Poisson distributed number with patch- and time-specific mean $\bar{\Lambda}_{i,t}$. For each generation, $\bar{\Lambda}_{i,t}$ is drawn itself from a log-normal distribution with mean λ and standard deviation σ . The latter determines the magnitude of environmental fluctuations, i.e., annual fluctuations in growth conditions. According to Hassell's model the newborn individuals survive with a certain probability (*s*), calculated as

$$s = \frac{1}{1 + aN_{i,t}}$$

with

$$a = \frac{\lambda - 1}{K_i}.$$

$N_{i,t}$ represents population size in patch *i* at time *t*, and K_i = habitat capacity of patch *i*. After all individuals mature, they emigrate with their individual dispersal propensity *d*, which is calculated as the arithmetic mean of its two alleles at the dispersal locus. One of these alleles is inherited from each of its parent. Alleles can mutate with a probability of 0.001. In case of mutation allele values are changed by adding a random number drawn from a Gaussian distribution with mean zero and standard deviation 0.2. At the beginning of simulations, the individuals' alleles were initialized as random numbers from a uniform distribution between 0.05 and 0.15. We tested additional distributions of initial values, but these had no qualitative influence on the results. We assume nearest neighbor dispersal, i.e., the destination patch is randomly chosen among the eight habitat patches, that surround the natal one. However, we assume a certain dispersal cost, i.e., an emigrant dies with probability μ_i . At the end of each generation, we implemented the occurrence of environmental catastrophes, i.e., the populations in every patch go extinct with probability ϵ_i independent of the actual population size.

Environmental gradients are applied linearly in space, starting with favorable conditions that allow the species' survival and reproduction (see standard values that follow). Along the *x*-direction of the metapopulation grid, one parameter (either K_i , λ_i , ϵ_i , or μ_i) changes

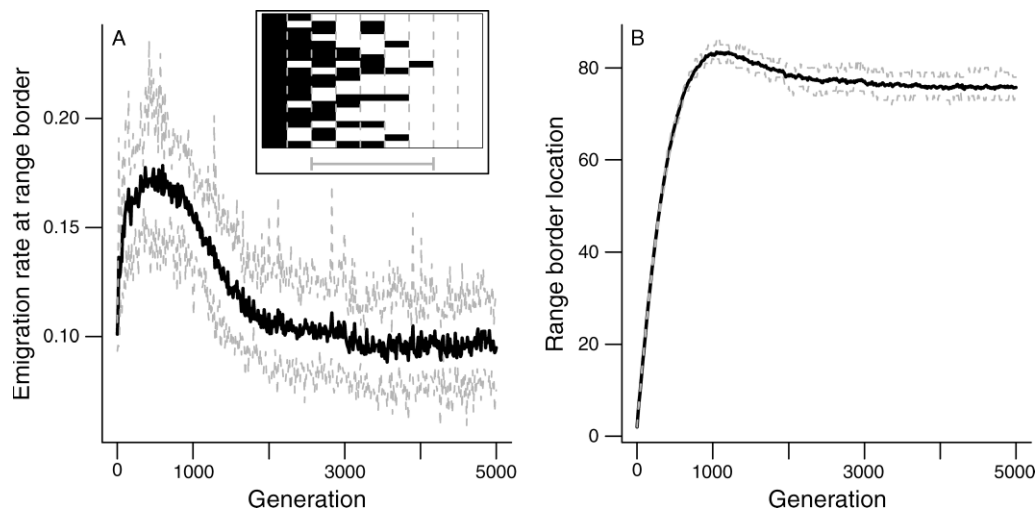


FIG. 1. (A) Change in mean emigration rate (the number of emigrating individuals divided by the population size before the dispersal event) at the range border and (B) range border position (1–100) in the μ -gradient over time. Shown are the results of 20 replications, with black lines indicating the mean, and gray lines the 5% and 95% quantiles. The schematic inset in panel A shows the occupancy of patches at the edge of the metapopulation's range. The gray bar indicates the zone over which emigration rates were averaged, i.e., all patches in the y dimension of the last five stripes of the gradient counted from the most-forward occupied patch. The probability of dispersing increases rapidly at the expanding wave front. After settling into a static distribution, selection leads to a decrease in emigration rate, resulting in a contraction of the range.

linearly from standard conditions ($K_i = 100$, $\lambda_i = 4$, $\varepsilon_i = 0.05$, $\mu_i = 0.2$) to conditions that do not allow the persistence of populations ($K_i = 1$, $\lambda_i = 0$, $\varepsilon_i = 0.5$, $\mu_i = 1$). The magnitude of environmental fluctuations σ was set to 0.5 for all simulations. Such values have already been successfully fitted to empirical data of natural insect populations (e.g., Nowicki et al. 2009) and were used in other theoretical studies as well (e.g., Travis et al. 1999, Poethke and Hovestadt 2002).

To simulate range expansion only the patch stripe with the most favorable conditions at $x = 1$ was initially occupied with individuals. During the next 5000 generations, the species was allowed to expand its range. We defined the range border as the stripe containing the most forward occupied patch. Data from the five most forward patch stripes behind the range border were pooled and analyzed to gain values for the mean emigration probability at the margin during the simulations (see inset in Fig. 1). To calculate the fraction of emigrants, the number of emigrating individuals was determined at the range border each generation and divided by the total population size before dispersal. For each parameter combination simulations were repeated 20 times each. All graphics were generated using the R language for statistical computing, version 2.9.2 (R Development Core Team 2009).

RESULTS

For all types of gradients the mean emigration probability increased during the phase of range expansion.

The left panel of Fig. 1 shows the increase in emigration probability at the range border over time for the dispersal mortality gradient: values increase from about 0.09 at the beginning to a maximum of approximately 0.17 during invasion. Yet once the expanding front reached the areas of high dispersal mortality, emigration probability reduced again. It can be seen, that in parallel with this decrease in dispersal the range of the species contracts. The final range was formed at a position in the gradient, where dispersal mortality was 0.81. In the other gradients, the range stabilized at the following values: $K = 14$, $\lambda = 1.13$, $\varepsilon = 0.33$.

In Fig. 2, we show the evolution of emigration rates plotted against the range border location only for the 10 outermost patch stripes behind the maximum possible range. In the gradient of dispersal mortality (left top panel) emigration rates during range expansion were higher than in the range core, but fell below core values once the maximum range expansion was reached. The emigration rates in the growth rate gradient (right top panel) also decreased after range settlement, but the effect on the range border location is rather low. Again, during range expansion the emigration rate at the range border exceeded that in the core habitat, but fell below it once the expansion stalled. For the gradient in patch capacity and especially for the extinction rate gradient migration rates continued to increase over the whole simulation time (two bottom panels). We did not observe a contraction of the range for either scenario.

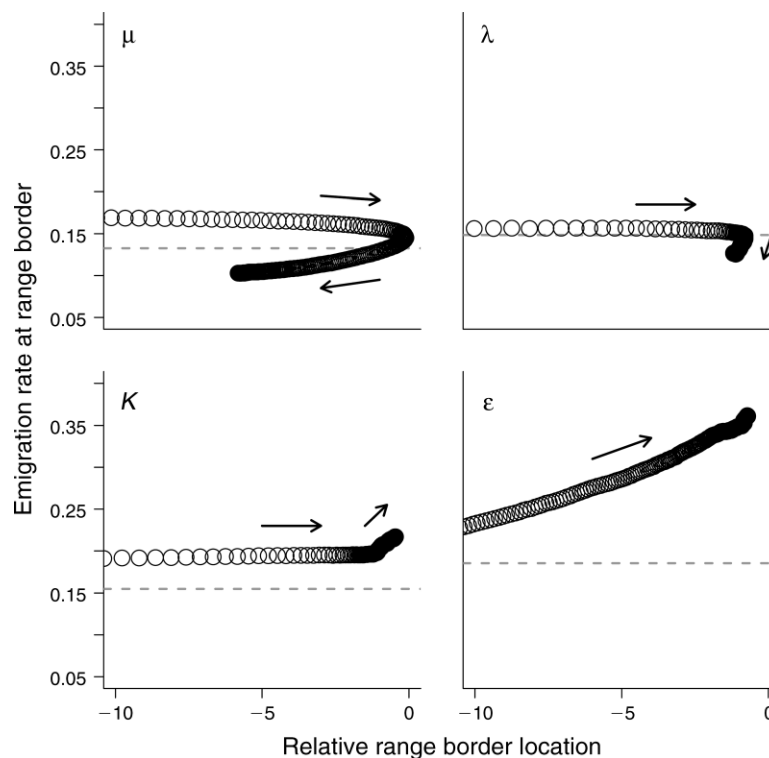


FIG. 2. Emerging emigration probabilities in the range border zone (see inset in Fig. 1) plotted against the range border location for all four gradients: μ , dispersal mortality; λ , per capita growth rate; K , patch capacity; and ϵ , extinction rate. The spatial location is set to zero for the maximum measured range for each case of gradient. Arrows indicate the direction of progression in time; data are plotted every 10 generations. Gray lines denote the mean emigration rate measured in the range core at the end of the simulations. The data shown are the average of 20 replicates for each scenario. To smooth the line, a moving average with a window of 50 data points was calculated.

In both cases the emigration rates at the expanding wave front exceeded those in the range core.

DISCUSSION

We have shown that Holt's prediction about range contraction following an initial phase of expansion only holds under special circumstances. In a gradient of dispersal costs, the range indeed showed strong elasticity. A growth rate gradient led to a similar, but less pronounced, effect. On the other hand, in simulations with gradients of carrying capacity or extinction rate, range contractions did not emerge at all, instead an ongoing increase in range size occurred. We trace the difference across the four scenarios to the fact that, in the former two (μ and λ gradient), emigration rates evolve to lower levels at the margin compared to the core region once the range expansion is over. In the latter two, however, dispersal at the margin is maintained at higher levels, even after the expansion has stalled. We thus conclude that a decline in emigration is the precondition for the phenomenon of elastic range borders, caused by a decrease in the recolonization

probability of extinct patches (as described, e.g., by Holt et al. 2005, Oborny et al. 2009).

In the dispersal mortality and the growth rate gradient, dispersal initially is highly beneficial due to the colonization of empty sites. Once established, however, populations persist well in these scenarios. After range expansion there are thus only few chances to colonize empty patches, consequently the dispersal benefit declines when the expansion phase is over and selection increasingly acts against high emigration. In comparison, in the gradient of growth rate extinctions caused by demographic stochasticity are more likely to happen than in the μ gradient, leading to a higher patch turnover. Hence, dispersal remains more favorable and this in turn weakens the elasticity effect.

For the gradients in carrying capacity and extinction rate the opposite is true. Both gradients lead to an increase in patch turnover due to the extinction of local populations, hence increasing the benefits of dispersal due to bet-hedging (distribution of risk; Philippi and Seger 1989, Ronce 2007). In the K gradient this is caused by the declining patch capacity that introduces strong

demographic stochasticity (Hanski and Gilpin 1997). The emigration rates in the K gradient increased much more slowly than in the other case. This can be explained by a lack of mutants, necessary for fast evolution, as total population sizes become very small at the range margin. This is not the case in the ϵ gradient. Although patches went extinct every three to four years near the final range border region ($\epsilon \approx 0.33$), inhabitants of newly colonized patches have a high fitness and many offspring, leading to enough mutants to allow rapid evolution for dispersiveness.

To answer the question, whether the fall in dispersal following range expansion in the μ and the λ gradient is based on evolution in marginal populations, we ran additional experiments and set the mutation rate to zero, when the outermost range position was reached. This had no qualitative influence on the results, indicating that the described fall results from expansion of lower dispersal strategies from the core to the margin.

To test the robustness of our results we ran additional simulations with different standard values for habitat capacity K (except for the K gradient). We found that range size increases initially with habitat capacity, yet that the effect levels off at a capacity of 100, where demographic stochasticity plays a little role for patch extinction. Additionally, for smaller values of K , elasticity was lower than for larger patches. Small patches suffer elevated demographic extinction risk leading to a reduction in range size as other conditions get harsher. However, frequent extinction due to demographic stochasticity introduces an added benefit to dispersal (like externally driven extinction risk) and hence favors the maintenance of high emigration probabilities. This does not change much after the expansion phase is over and we thus observed a rather minor reduction in emigration in scenarios with low K values. As the range border elasticity directly depends on the difference between dispersal rate during range expansion and after stabilization, the range contracted less. Further tests of the influences of environmental stochasticity and external extinction rate on our simulations showed similar results for all gradients.

In our study, we used nearest neighbor dispersal in a grid-based model. However, Dytham (2009) did not observe a strong effect on the evolving mean dispersal distance along various habitat gradients tested, except for a gradient that directly affected the distance specific costs of dispersal. Distances emerging would usually lead to nearest neighbor dispersal (see Bartoń et al. 2009). We thus assume that simulations with evolving dispersal kernels would not fundamentally alter the conclusion we draw in this manuscript.

Range contractions are hard to detect in field studies (Thomas et al. 2006) and are even harder to explain once they are found (Channell and Lomolino 2000). However, as we showed it is possible that some of these

range contractions might not be caused by temporal changes in the environment, but occur in the aftermath of historical range expansions, at least in gradients that favor lower emigration rates at the range margin than in the core area. Yet in nature, gradients are unlikely to occur independently from each other. Especially a habitat fragmentation gradient (represented by μ in our study) will frequently coincide with a decline in patch size/patch quality, what might blur the effect of the fragmentation on dispersal evolution. Nonetheless we expect the phenomenon of elastic ranges to occur in nature with increasing frequency in light of the ongoing climatic change that promotes shifts in range boundaries. Recent studies showed that the changing climate is expected to have strong influences on species' range shifts, leading to an increase in invading species (Parmesan 2006).

This study highlights the importance of investigating non-equilibrium situations in range formation processes. To be able to gain better predictions of species' future distributions in time and space and improve conservation strategies we need to focus research on transient states, as most geographic ranges are unlikely to be in equilibrium.

ACKNOWLEDGMENTS

A. Kubisch was supported by a grant from the German Science Foundation (Poethke DFG PO 244/4-1), and T. Hovestadt by project CLIMIT funded by the FP6 BiodivERsa ERA-NET. We thank two anonymous reviewers for helpful comments on the manuscript.

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