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The downward spiral: eco-evolutionary feedback loops lead to the emergence of 'elastic' ranges

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Abstract

In times of severe environmental changes and resulting changes in the geographical distribution of animal and plant species it is crucial to unravel the mechanisms responsible for the dynamics of species' ranges. Without such a mechanistic understanding reliable projections of future species distributions are difficult to derive. Species' ranges may be highly dynamic and subject to 'elastic' behavior, i.e. a range contraction following a period of range expansion as a consequence of eco-evolutionary feedbacks due to (rapid) dispersal evolution. It has been proposed that this phenomenon occurs in habitat gradients, which are characterized by a negative cline in selection for dispersal from the range core towards the margin, as one may find with increasing patch isolation, for example. Using individual-based simulations and further numerical analyses we show in this study that the presence of Allee effects is a necessary condition for ranges to exhibit elastic behavior. The eco-evolutionary interplay between dispersal evolution, Allee effects and habitat isolation lead to the emergence of decreased colonization probability and increased local extinction risk after range expansion, which result in an increasing amount of marginal sink patches and thus range contraction. The nature of the gradient is crucial, as gradients which do not select for lower dispersal at the margin than in the core (especially patch size, demographic stochasticity and extinction rate) did not lead to elastic range behavior. Thus, we predict that range contractions are likely to occur after periods of expansion for species living in gradients of increasing patch isolation, which suffer from Allee effects.

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Introduction

Currently, an important number of species' ranges has come under pressure through global climatic, environmental and socio-economic changes (Walther et al., 2002, Perry et al., 2005, Chen et al., 2011, Bellard et al., 2013). It is now well documented that such range shifts often exhibit subsequent fundamental shifts in (meta-)population dynamics (Altermatt et al., 2008, Thomas, 2010). If we intend to assess and predict the impact of these global changes (Stocker et al., 2013) an adequate understanding of range dynamics is crucial. Yet, our understanding of the formation of species' ranges is still limited, as both biotic and abiotic ecological and rapid evolutionary processes affect range formation in complex ways (Kubisch et al., 2014).

Besides simply expanding or contracting, species' ranges may also exhibit more complex dynamics such as 'elastic' behavior. Elasticity (as described by Kubisch et al., 2010) implies that a range expansion is immediately followed by a period of contraction due to evolutionary changes in dispersal. In his review of the work of MacArthur (1972), Holt (2003) first described this phenomenon. He argued that after a period of increasing dispersal during range expansion there can be substantial selection against dispersal in marginal areas due to source-sink dynamics. If invasions occur along a fitness gradient from source to sink populations, which can for example be due to increasing habitat fragmentation or to a mismatch in local adaptation, sink populations would be sustained by initially high emigration rates which are selected for during such expansions in general (Phillips et al., 2010, Shine et al., 2011, Kubisch et al., 2013). Subsequent selection against dispersal due to exactly these sink habitats will result in a contraction of the geographical range.

In a simulation study, Kubisch et al. (2010) could show that this phenomenon may indeed be likely to occur in nature, but that it crucially depends on the nature of the underlying gradient. The authors concluded that the mechanism explaining range elasticity is selection for lower emigration rates at range margins relative to core areas

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which can be due to increasing patch isolation, for example. In more recent work Henry et al. (2013) suggested that elasticity should also be found in other types of gradients, if one takes into account the evolution of dispersal distance. We here revisit the results of Kubisch et al. (2010) and Henry et al. (2013) in detail and clarify the impact of dispersal strategies and the nature of the habitat gradient.

Following the argumentation by Holt & MacArthur, a crucial determinant of range border elasticity is the presence of actual sink patches at the initial wide range after expansion (as was already noted by Kubisch et al., 2010). A sink population, i.e. a population with negative growth rate, is likely the result of demographic Allee effects (i.e. reduced growth rates at low population sizes or densities, Courchamp et al., 2010). Here we argue that a negative cline in selection for dispersal from the range core to the margin is only one prerequisite for range elasticity, and that the presence of Allee effects leading to sink populations at range margins is the second. The eco-evolutionary feedback loop created by these two forces leads to a spatio-temporally non-linear cline in immigrant fitness, which is caused by the emergence of sink patches and finally results in range contraction. Figure 1 shows a schematic representation of the interactions between dispersal, colonization, local extinction and Allee effects in shaping the range of a species (compare also Kubisch et al., 2014).

The Model

Landscape and individuals

We use an individual-based model of a spatially structured (meta-)population of an asexually reproducing species with discrete generations. This approach has been used in several studies before (Poethke et al., 2011, Fronhofer et al., 2013, Kubisch et al., 2014). The simulated landscape consists of $x \cdot y = 200 \cdot 50$ habitat patches, arranged on a rectangular grid. Every patch may contain a population of the species, assuming

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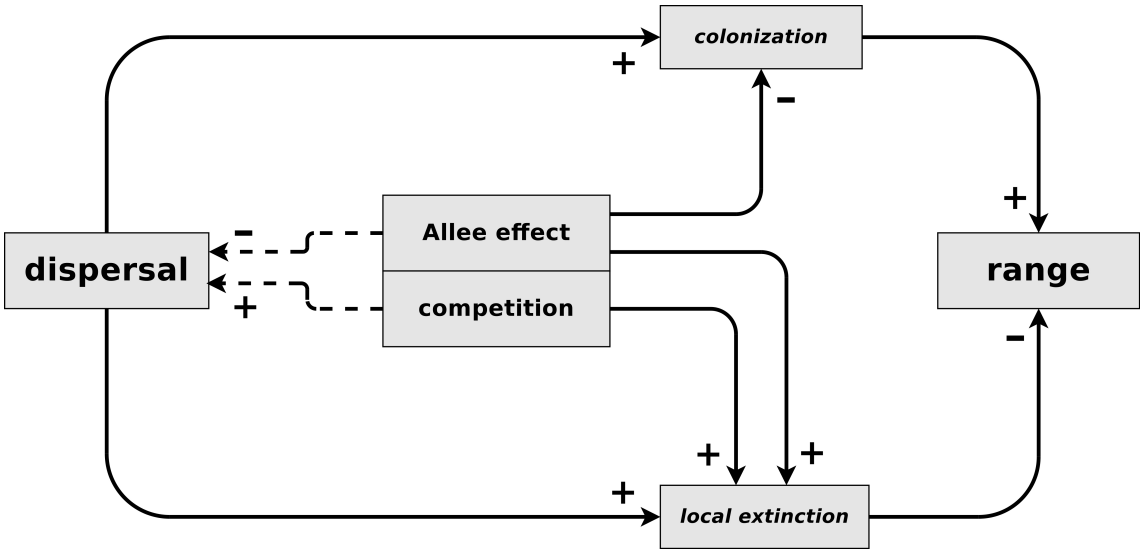

Figure 1: A schematic representation of the ecological (solid lines) and evolutionary (dashed lines) of Allee effects and competition on dispersal, colonization and local extinction, which finally determine the position of a range border. Following the metapopulation approach of Kubisch et al. (2014), stable range limits are the consequence of an equilibrium between colonization and extinction (see also Oborny et al., 2009), both of which are strongly influenced by dispersal. While competition (among kin or in general) leads to an evolutionary increase in dispersal, what is also the basis for increasing dispersal during range expansions, Allee effects lead to selection against dispersal, as they increase local extinction probability and decrease colonization. To understand the elasticity of range limits during periods of expansion, one hast to keep in mind that during range expansion, competition is the driving force for dispersal evolution, while in the aftermath the prevailing Allee effect dominates the evolution of dispersal – resulting in a contraction of the range. To investigate this hypothesis we use an individual-based model very similar to that used by Kubisch et al. (2010), but focus on the presence and strength of demographic Allee effects.

a carrying capacity $K_{x,y}$ (see below). Local populations consist of individuals, which are determined by their specific location x, y and one heritable trait defining their probability to emigrate. At initialization, dispersal alleles are randomly drawn from a uniform distribution between 0 and 1.

To allow for range formation, we implement linear unidirectional environmental gradients. This means that along the x-axis of the landscape, one specific habitat characteristic changes from favorable to unfavorable conditions with respect to the survival of the species (see below for details).

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Population dynamics

Local population dynamics follow the discrete logistic growth model developed by Beverton and Holt (1957). This model is extended by the implementation of a direct Allee effect, the strength of which depends on population density instead of size (see also Kubisch et al., 2011). We draw the individuals' average offspring number for every patch and generation ($\overline{\Lambda_{x,y,t}}$) from a log-normal distribution with mean $\lambda_{x,y}$ and standard deviation σ. The latter thus represents the degree of environmental stochasticity. Afterwards every individual in a patch gives birth to a number of offspring drawn from a Poisson distribution with mean $\overline{\Lambda_{x,y,t}}$. Due to density-dependent competition offspring survive with a certain probability s, which is given by

$$s_{x,y,t} = \frac{b}{1 + a \cdot N_{x,y,t}}, \tag{1a}$$

$$with \quad a = \frac{\lambda_{x,y} - 1}{K_{x,y}}, \tag{1b}$$

$$b = \frac{(N_{x,y,t}/K)^2}{(N_{x,y,t}/K)^2 \cdot \alpha^2} \tag{1c}$$

with $K_{x,y}$ being carrying capacity of a patch, $N_{x,y,t}$ denoting the population size of a focal patch and α defining the strength of the Allee effect. We assume a sigmoid increase in survival probability with the number of inhabitants in a patch (see eq. 1c). Individuals in a population at density $\frac{N_{x,y,t}}{K_{x,y}} = \alpha$ will thus have a decrease in their survival of 50 %.

A newborn inherits the dispersal allele from its parent, which may mutate with probability $m = 10^{-4}$ by adding a Gaussian distributed random number with mean 0 and standard deviation 0.2.

Following reproduction, every population may go extinct by chance with probability

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$\epsilon = 0.05$.

Dispersal

Surviving offspring emigrate with a probability that is given by their dispersal allele. If an individual disperses, it may die with a certain probability μ, which is calculated as the arithmetic mean between the patch-specific dispersal mortalities $\mu_{x,y}$ of the natal and the target patch. The target patch is randomly drawn from the eight surrounding patches. Dispersal mortality includes all potential costs that may be associated with dispersal, like e.g. predation risk or energetic costs (Bonte et al., 2012). To avoid edge effects we wrap the world in y-direction, thus forming a tube along the x-dimension of the world. Individuals leaving the world along the x-dimension are reflected.
To test the validity of our results against alternative implementations of dispersal we performed additional simulations with dispersal distances evolving instead of propensities. In these cases the dispersal alleles coded for the mean of a negative exponential distance distribution (see also Henry et al., 2013). Given that the dispersal mortality μ in our original approach means a per-step mortality (as the step length for nearest neighbor dispersal is one) we have based the implementation of mortality in the kernel scenario on the same rationale and assumed that the probability of dying during the transition phase, μ_d, is given by:

$$\mu_d = 1 - exp(-\mu \cdot d) \tag{2}$$

with d denoting the traveled dispersal distance (for more details see Fronhofer et al., 2015). We repeated all simulations for these alternative scenarios and provide the results in the supplementary material.

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Experiments and analysis

In order not to bias the results in any direction by using artificial initial values for the dispersal traits we implemented a burn-in period allowing for the adaptation of dispersal strategies to local conditions in the range core. Therefore we added additional 10 rows to the landscape in front of the position $x = 1$, all patches there being defined by conditions found at position $x = 1$ and filled these patches with $K_{1,y}$ individuals. We then let the simulation run for $2,500$ generations, assuming torus conditions of the burn-in region (i.e. individuals leaving this region in x- and y-direction were wrapped around). In the case of dispersal propensities evolving the alleles were drawn from a uniform distribution between 0 and 1. In the alternative scenario with dispersal distances evolving we initialized the individuals with mean dispersal distance values from a uniform distribution between 0 and 10. Note that dispersal distances never evolved to such high values that our burn-in region could have been too small. Afterwards, the simulation was run for $5,000$ generations, assuring the formation of a stable range border. Although we focus on a gradient in dispersal mortality (i.e. habitat isolation), we tested a range of other possible gradients from favorable ($K_{1,y} = 100$, $\lambda_{1,y} = 4$, $\mu_{1,y} = 0.2$, $\sigma_{1,y} = 0$, $\epsilon_{1,y} = 0$) to unfavorable conditions ($K_{200,y} = 0$, $\lambda_{200,y} = 0$, $\mu_{200,y} = 1$, $\sigma_{200,y} = 10$, $\epsilon_{200,y} = 1$). These results can be found in the Supplementary material, Appendix 1, Fig. A1 – A4. Respective parameters, which were not changing across space in a given simulation were set to standard values ($K_{x,y} = 100$, $\lambda_{x,y} = 2$, $\mu_{x,y} = 0.2$, $\sigma_{x,y} = 0.2$, $\epsilon_{x,y} = 0.05$). To account for the fact that fragmentation gradients, as they occur in nature, usually affect not only the isolation of habitat patches, but also imply decreasing patch sizes, we have additionally tested a 'mixed' gradient, in which along the x-axis habitat capacity K was reduced and dispersal mortality μ increased, using the same parameters as given above. These results can be found in the Supplementary material, Appendix 1, Fig. A5. We tested 11 values for the strength of the Allee effect (α) in equidistant steps from 0 to 0.1. For

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all scenarios we performed 50 replicate simulations.

To quantify the presence and degree of range elasticity we analyzed range border position as a function of time. We fitted a function to the resulting progression of relative range size r, which is calculated as the absolute range size position along the landscape's x-dimension R divided by the maximum extent of that dimension ($x_{max} = 200$). The function we used (eq. 3) is flexible enough to quantify elasticity and it's parameters can be directly interpreted in biological terms:

$$r = 1 - exp(-v_e + t) \cdot x_{max} \cdot \left(\tilde{r} + \frac{1 - \tilde{r}}{1 + exp\left(\frac{4 \cdot v_c \cdot \Delta_t}{1-\tilde{r}} - \frac{4 \cdot v_c \cdot t}{1-\tilde{r}}\right)} \right) \tag{3}$$

with v_e denoting the speed of range expansion, $\tilde{r}$ the equilibrium range size, v_c the speed of range contraction and Δ_t the time to reach equilibrium. Using non-linear least squares regressions (R language for statistical computing version 3.1.0 function nls(), Team, 2013) we fit the curve to the respective simulation output. The relative amplitude of the elasticity effect was calculated using the resulting function as:

$$A = \frac{max(r) - \tilde{r} * x_{max}}{max(r)} \tag{4}$$

Figure 2 shows a typical example of this calculation.

Numerical analysis of the mean fitness of colonizers

To mechanistically investigate the eco-evolutionary feedback loop underlying the observed range dynamics, we performed additional numerical analyses and quantified the mean fitness expectations of potential colonizers at the range margin as a function of their dispersal strategy and of the landscape gradient. In order to guarantee comparability, we calculate the colonizers' fitness expectations over one generation for every potential location of the range margin in close analogy to the individual-based simulation model detailed above:

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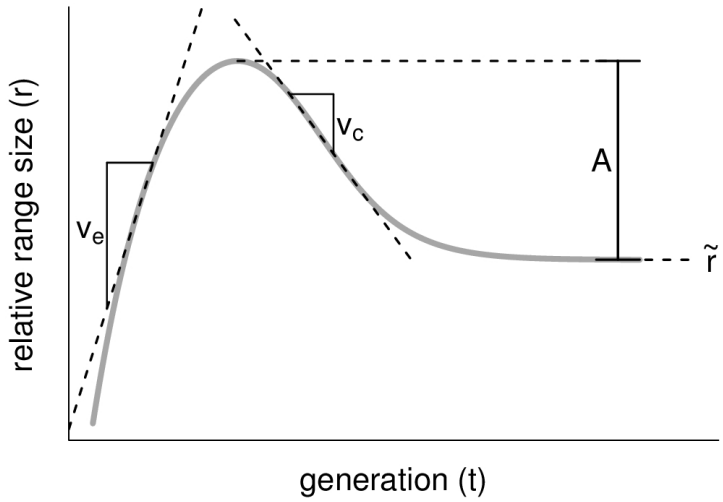

Figure 2: A sketch of the for elasticity typical relationship between relative range border position and time. The curve was created by using eq. 3 with the following parameters: $v_e = 0.0015$, $v_c = 0.0004$, $\Delta_t = 2000$, $\tilde{r} = 0.35$). The meaning of the four parameters used in the analysis is denoted.

1. We calculate the number of colonizers at the margin based on the conservative assumption that the range behind the margin is fully populated (i.e. all patches are at $N_{x,y,t} = K_x$). Thus the number of colonizers is given by $N_{c,x} = K_x \cdot d \cdot (1 - \mu_x)$, with d denoting emigration rate. Our approach is conservative in the sense that populations directly behind the margin may not yet have reached carrying capacity. We therefore overestimate the number of colonizers which leads to an underestimation of the impact of the phenomenon of interest, the Allee effect. 2. As described above for the evolutionary simulations we assume that the mean fecundities of these colonizers $\overline{\Lambda_x}$ follow a lognormal distribution with mean λ_x and standard deviation σ_x. The parameter σ accounts for environmental stochasticity. 3. Demographic stochasticity is taken into account by assuming that reproduction can be described as a Poisson process with $\overline{\Lambda_x}$ as mean. Subsequently, density regulation is applied according to 1 (with $N_{c,x}$ giving the necessary population size). 4. Finally, external extinctions are represented as a binomial process with mean $(1 - \epsilon)$ acting on the offspring numbers. This algorithm allows us to calculate a distribution W of potential per capita offspring numbers for each x-location in all gradients, assuming that the margin of a saturated

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range would lie directly in front of it. We approximated this distribution by sampling $1,000,000$ times. To average the mean colonizer fitness we used an approximated geometric mean calculation. The arithmetic mean would be a poor estimate of fitness, as it is comparably insensitive to the distribution's variance. The true geometric mean is, however, too sensitive against zero offspring numbers, which are drawn with a high probability based on above method. A Jean series approximation of the geometric mean, however, provides a sensible estimate, as it is sensitive towards variation but not zero, when such offspring numbers are included. According to Jean and Henry (1983) we calculate the mean colonizer fitness $\overline{w_c}$ thus as:

$$\overline{w_c} = exp\left(log\left(\overline{W} - \frac{var(W)}{\overline{W}^2}\right)\right) \tag{5}$$

with $\overline{W}$ denoting the arithmetic mean of the distribution.

We performed this analysis for all gradients and two values for Allee effect strength ($\alpha = 0$ and $\alpha = 0.05$). We varied emigration rate d in 10 equidistant steps from 0.05 to 0.5.

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Results

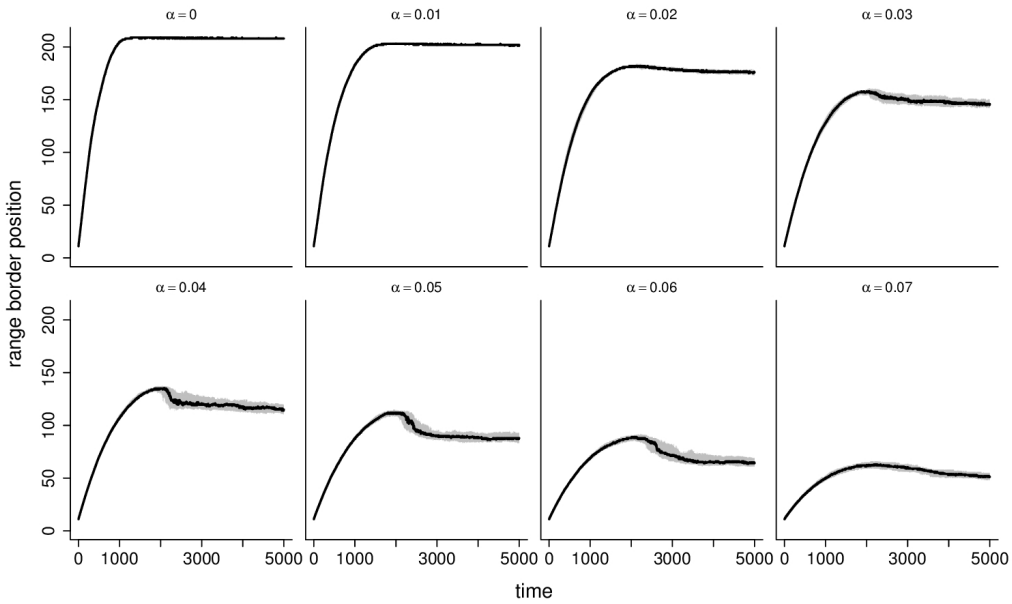

Figure 3: Range border position as a function of simulation time for a gradient in dispersal mortality (μ). Allee effect strength increases from the top left to the bottom right panel. For parameter values see main text. The black lines show the median values of 50 replicate simulations, the shaded grey areas denote 25% - and 75% quantiles.

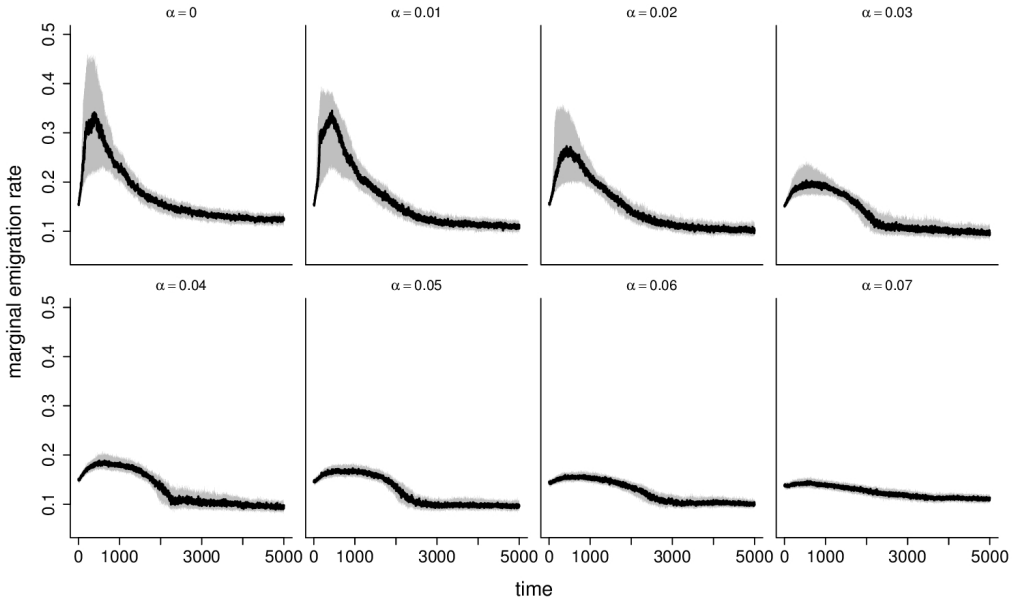

Figure 4: Marginal emigration rate as a function of simulation time for a gradient in dispersal mortality (μ). Allee effect strength increases from the top left to the bottom right panel. For parameter values see main text. The black lines show the median values of 50 replicate simulations, the shaded grey areas denote 25% - and 75% quantiles.

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Strong elasticity was only detected for a gradient in dispersal mortality, i.e. patch isolation, in the presence of an Allee effect (Fig. 3). We found a very weak elastic behavior in a gradient of decreasing per capita growth rate (Supplementary material Appendix 1, Fig. A2) — a result consistent with the findings in Kubisch et al. (2010). All other gradients (K, σ, ϵ) did not lead to range border elasticity (Supplementary material Appendix 1, Fig. A1, A3, A4). Importantly, elasticity only occurred in the presence of an Allee effect and the degree of elasticity (amplitude) increased with increasing Allee effect strength (Fig. 3). For values of α exceeding 0.07, the entire spatially structured population went extinct. It is also important to note that we did find elastic ranges for a mixed gradient - scenario, including declining patch size and increasing patch isolation (Supplementary material Appendix 1, Fig. A5).

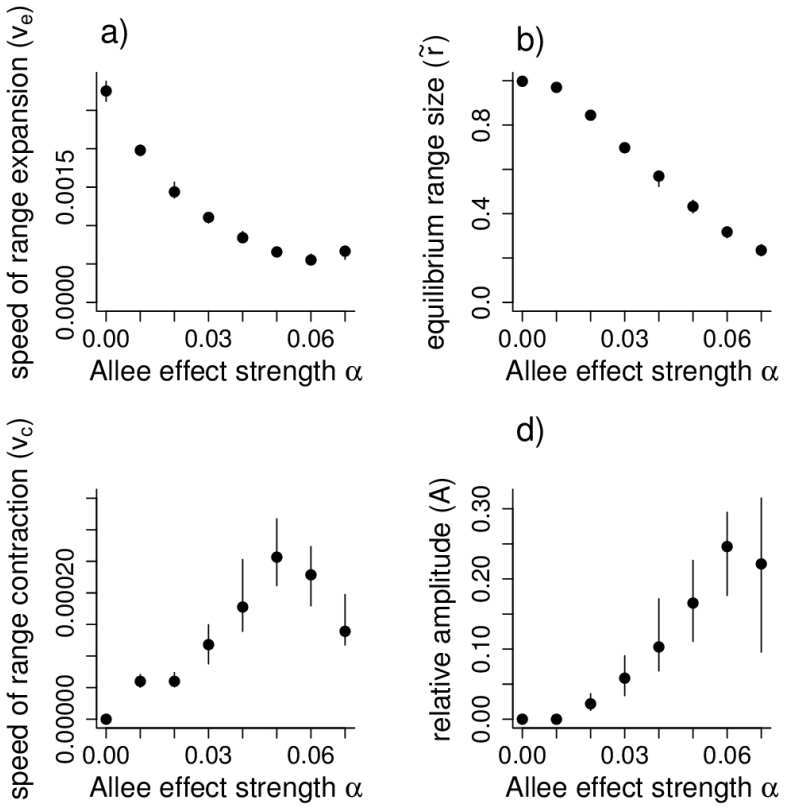

Figure 5: Results of the quanitative analysis of elasticity depending on Allee effect strength. Shown are (a) the speed of range expansion, (b) the relative range size, (c) the speed of range contraction and (d) the relative amplitude of the elastic range effect. Shown are median values of 50 replicate simulations, error bars denote 25%- and 75%-quantiles.

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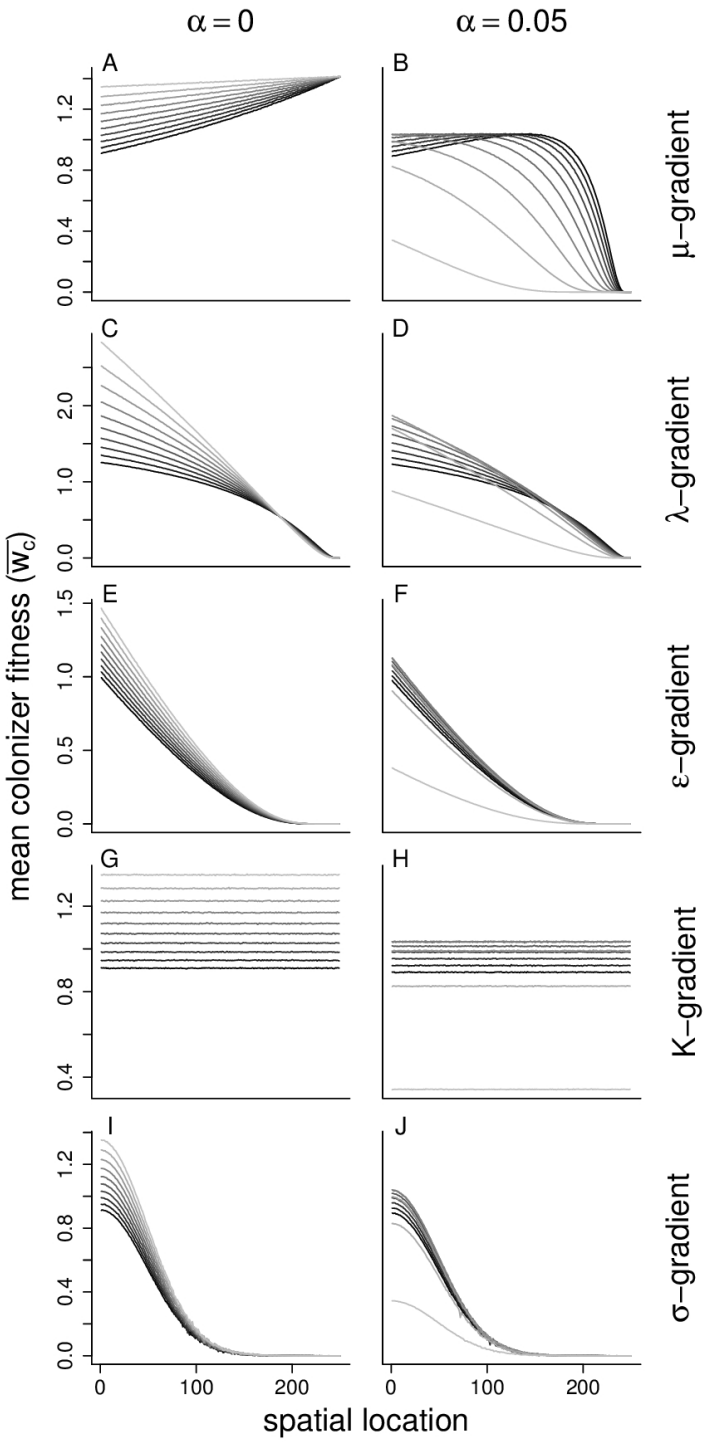

Figure 6: Results of the numerical analyses of mean colonizer fitness as a function of the Allee effect strength (α), landscape characteristics and emigration rate. Shown is the approximated geometric mean per capita offspring number to be expected for colonizers arriving at every potential x-location under the assumption that the species' range ends right before each position (see main text for details). Line coloring refers to the rate of dispersal, which decreases from 0.5 (black) to 0.05 (lightest gray) in 10 equidistant steps.

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The evolving mean emigration propensity at the range margin was negatively affected by the Allee effect strength (Fig. 4). Consequently, with increasing Allee effects range expansion was slower (Fig. 5a) and the resulting relative range size was smaller (Fig. 5b). The enhanced elasticity for increasing Allee effects, which is apparent in Fig. 3, was characterized by (i) an increase in the velocity of contraction, followed by a slight decrease for a very strong Allee effect (Fig. 5c) and (ii) an increase in the amplitude, i.e. the difference between maximum and equilibrium range size (Fig. 5d). As we had hypothesized, a considerable Allee effect must be present for elasticity to emerge ($A > 0$ for $\alpha \geq 0.02$, Fig. 5d).

The results of simulations allowing for the evolution of dispersal kernels instead of propensities showed the same qualitative behavior of the system. Still remarkable elasticity could only be found in a gradient of dispersal mortality, in this case meaning a per-step mortality, and for strong Allee effects (Supplementary material Appendix 2, Fig. A6 - A10).

The numerical analyses of mean colonizer fitness show characteristically different patterns between the various environmental gradients (Fig. 6). For dispersal mortality gradients without Allee effects an increase in colonizer fitness deeper in the gradient can be observed (Fig. 6A), which sets this gradient apart from all the others. Increasing dispersal (darker lines) results in overall lowered fitness expectations (Fig. 6A). Allee effects strongly interact with this pattern (Fig. 6B): for high dispersal rates the relationship between colonizer fitness and spatial location changes from monotonically increasing to unimodal with a rapid decrease of fitness in regions with harsher conditions (i.e. higher dispersal mortality; Fig. 6B). The lower the dispersal rate is, the sooner this decrease sets in.

This dramatic impact of Allee effects on the spatial distribution of colonizer fitness is strictly associated with scenarios in which (strong) range border elasticity could be observed (mortality and fecundity gradients see Fig. 3, A2).

For all other gradients, we either found patterns of decreasing fitness deeper in the

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gradient (Fig. 6C-F,I.J) or no spatial relationship in the case of the gradient in carrying capacity (Fig. 6G,H). However, for all these gradients we found the same impact of the Allee effect: whereas in its absence decreased dispersal rates (lighter colors in Fig. 6) resulted in consistently higher fitness, an Allee effect inverted this pattern. Importantly, no non-monotonic effects could be found in contrast to the results for dispersal mortality (Fig. 6A and B; and fertility to a smaller extent, Fig. 6 C and D).

Discussion

Our results show that an eco-evolutionary feedback loop, caused by the interplay between Allee effects, landscape structure and dispersal evolution, is necessary for ranges to show elastic behavior. As a range expansion proceeds into an isolation gradient, the selective pressures at the range margin change: Initially, spatial selection (more dispersive individuals being at the front in combination with fitness benefits through reduced competition; Phillips et al. 2010) leads to the evolution of increased dispersal. Yet, once the range has expanded more deeply into the gradient, dispersal is selected against because of high habitat isolation and decreases (Fig. 4). As a result of this decrease, more and more patches turn into sinks because of the presence of the Allee effect. This leads to a range contraction (Fig. 3). The strength of this effect is further increased due to selection against dispersal as a result of source/sink-dynamics — a downward spiral of selection against dispersal leading to the observed strong range contraction.

The fitness-relevant result of these non-linearly interacting effects can directly be seen in Figure 6B. High dispersal rates due to spatial selection (dark lines) lead to a fast range expansion, as colonizer fitness is initially increasing or at least not decreasing over space. At a certain point in space — defined by an interaction between gradient steepness, dispersal rate and Allee effect strength — colonizer fitness drops abruptly.

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This selects against dispersal and leads to the fitness profiles depicted in light grey colors. These increasing fitness decreases at the range margin finally lead to a (strong) range contraction. These dynamics can only be observed in mortality gradients and to a smaller extent also in fertility gradients (Fig.6D). All other gradients (Fig. 6 E-J) do not show such an abrupt change in the spatial fitness expectations and mostly exhibit decreasing colonizer fitness early on. This implies that range border elasticity cannot be found in these latter gradients.

The negative relationship we find between range size and Allee effects as well as the speed of range expansion and Allee effects is in good accordance with previous theoretical studies. Keitt et al. (2001) for example showed using reaction-diffusion models and ordinary-differential-equation models that for a wide range of biologically plausible conditions Allee effects may not only slow down invasions, but lead to the formation of stable range limits through invasion pinning. A good overview of the topic is provided by the literature review of Taylor and Hastings (2005), who summarize known effects of Allee effects on invasions, both from the side of theory and empiry. In our results the speed of range contraction and the amplitude increase in concert with stronger Allee effects, which implies that under these conditions the phenomenon of elasticity is most prominent (see Fig. 5). Note that the findings of Kubisch et al. (2010) were caused by an Allee effect, too. The authors modeled a species with sexual reproduction, thus implicitly assuming a mate-finding Allee effect. In summary, elasticity can be found if two conditions are fulfilled: 1) dispersal must be selected against at the range margin which leads to stable ranges (Kubisch et al., 2010) and 2) a (strong) Allee effect will lead to a subsequent contraction, i.e. elasticity (Fig 2,3). Note that elastic ranges might even be observed in more natural gradients of fragmentation, in which not only patch isolation increases, but patch size also decreases (Fig. A5). Although lower patch sizes imply increased demographic stochasticity and thus selection for increased dispersal at the range margin, this selective force is outweighed by the strong selection for lower dispersal due to its increased costs.

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To test the validity of our findings under the assumption of evolving dispersal distances instead of mere propensities we performed additional simulations using negative exponential dispersal kernels in analogy to Henry et al. (2013). These simulations demonstrate the qualitative robustness of our results with respect to the evolution of dispersal distances, as elasticity was again only found in scenarios with gradients in dispersal mortality and strong Allee effects (Supplementary Material; Figs. A6-A10). Yet, very weak elasticity can also occur in fertility gradients.

These results seem to be at odds with recent findings reported by Henry et al. (2013). These authors report that range elasticity might also be a consequence of climate change and occur independently of an underlying abiotic gradient. Henry et al. (2013) modeled a species' range shift, which was externally driven by the tracking of a window of climatic suitability. This window determined the range of the species. Thus, instead of a range expansion scenario in which the range border forms along a gradient, the shift in range position was externally triggered. Similar to what we describe in this study, the populations in that scenario evolved higher dispersal during the period of range shift. In fact, this was their only possible strategy to avoid extinction. Once climate change stopped the individuals continued to disperse further into unsuitable habitat as dispersal strategies were not assumed to be condition-dependent or plastic in any way. Subsequently, natural selection could act and lead to a reduction in dispersal at the range margin. Of course, this process is not instantaneous which leads to a time lag between the end of climate change and the optimal adaptation of dispersal strategies to the new conditions. During this time lag individuals continue to disperse outside their range which leads to strong source/sink-dynamics. As Henry et al. concluded, in such a scenario the nature of the gradient (patch isolation, patch size, resource availability etc.) is not a prerequisite for elasticity to occur. Indeed these additional gradients do not play an important role, as the dynamics of the range expansion are centrally governed by the climate window, which in fact represents the most extreme form of a mortality gradient (suitable-unsuitable). Furthermore, it is also

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clear that Allee effects do not need to be considered in such a scenario as individuals at the range margin immigrating into unsuitable patches will deterministically go extinct. Clearly, elastic ranges emerge due to selection against dispersal at the range margin and source/sink-dynamics. These conditions are automatically met in natural landscapes that are characterized by a gradient in fragmentation, for example. In addition, Allee effects are necessary to induce source/sink-dynamics at the range margin which will then lead to elasticity, as we show in this study. Alternatively, elasticity can be triggered externally, e.g. by moving climatic windows of habitat suitability, as reported by Henry et al. (2013). Note that in such a case the suitability window needs to advance rapidly enough to select for higher dispersal. Individuals need to disperse out of the suitability window and the limits of the suitability window need to be very steep in order to guarantee population extinction. If the latter condition is not fulfilled, we predict that Allee effects will again be required for elasticity to emerge.

Conclusion

With this study we show that elastic ranges are caused by the eco-evolutionary interplay between dispersal evolution at the range margin, habitat isolation and the presence of Allee effects. If one of these conditions is not fulfilled, i.e. if the Allee effect is not strong enough or if higher dispersal is selected for at the margin than in the core (as e.g. in gradients in patch size or demographic stochasticity), no range contraction after an expansion period is to be expected. These conclusions generally hold true as long as range expansions are not directly caused by rapid and strong climate change. We predict that in nature range contractions after expansions are most likely to occur in fragmentation gradients for species that reproduce sexually, show social behavior or are otherwise prone to suffer from an Allee effect.

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