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# Allee effects are necessary to explain the emergence of 'elastic' ranges

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## Abstract

In times of severe environmental changes and resulting shifts 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 we show in this study that the presence of Allee effects is a necessary condition for ranges to exhibit elastic behavior. A pronounced source/sink-structure at the range margin caused by Allee effects, leads to selection for decreased dispersal and subsequently to lowered colonization rates and increased local extinction risk. In addition, the nature of the gradient is crucial, as gradients which do not select for lower dispersal at the margin than in the core (patch size, growth rate, demographic stochasticity, extinction rate) did not lead to elastic range behavior. Thus, we argue 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). These impacts are predominantly mediated by changes in dispersal, which itself can be affected by climate change in multiple ways (Travis et al., 2013).

Besides simply expanding or contracting, species' ranges may also exhibit more complex dynamics such as 'elastic' behavior. Elasticity implies that a range expansion is immediately followed by 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 results 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

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underlying gradient. The authors concluded that the mechanism explaining range elasticity is selection for lower emigration rates at range margins relative to core areas 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, especially in the context of climate change. However, following the argumentation by Holt & MacArthur, a second 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 Model

## Landscape and individuals

We use an individual-based model of a spatially structured (meta-)population of a species with discrete generations. This approach has been used in several studies before (Travis et al., 1999, 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 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 the initialization of the simulations, we fill all patches at $x = 1$ with $K$ individuals. Dispersal alleles are at that time randomly drawn from a uniform distribution between 0 and 1.

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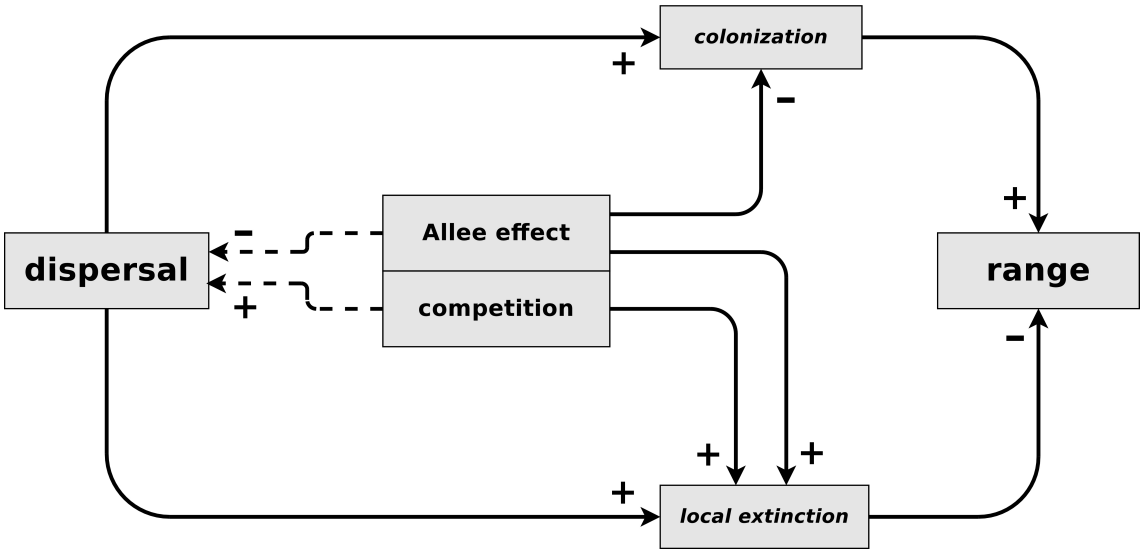


Figure 1: A schematic representation of the ecological (solid lines) and evolutionary (dashed lines) of Allee effects and competition on dispersal, colonization and local extinction, which finally determine the position of a range border. Following the metapopulation approach of Kubisch et al. (2014), 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.

To allow for range formation, we implement 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).

## 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

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deviation $\sigma$. 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 $\alpha$ 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.

At the end of each generation, every population may go extinct by chance with probability $\epsilon = 0.05$.

## 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 $\mu$, which is calculated as the arithmetic mean between the patch-specific dispersal mortalities $\mu_{x,y}$ of the natal and the target patch. This dispersal mortality includes all potential costs that may

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be associated with dispersal, like e.g. predation risk or energetic costs (Bonte et al., 2012). If an individual survives the transition phase, it randomly immigrates into one of the eight neighbouring habitat patches. 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.

## Experiments and analysis

As mentioned above, initially all patches at location $x = 1$ in the gradient were populated with $K_{1,y}$ individuals. 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 a decreasing patch size, we have additionally tested a 'mixed' gradient, in which along the x-axis habitat capacity $K$ was reduced and dispersal mortality $\mu$ increased, using the same parameters as given above. Also these results can be found in the Supplementary material, Appendix 1, Fig. A5. We tested 11 values for the strength of the Allee effect ($\alpha$) in equidistant steps from 0 to 0.1. For 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

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($x_{max} = 200$). The function we used (eq. 2) is flexible enough to quantify elasticity and it's parameters can be directly interpreted in biological terms:

$$r = 1 - exp(-v_e \cdot t) \cdot x_{max} \cdot \left( \tilde{r} + \frac{1 - \tilde{r}}{1 + exp\left(\frac{4 \cdot v_c \cdot \Delta_t}{1-\tilde{r}} - \frac{4 \cdot v_c \cdot t}{1-\tilde{r}}\right)} \right) \tag{2}$$

with $v_e$ denoting the speed of range expansion, $\tilde{r}$ the equilibrium range size, $v_c$ the speed of range contraction and $\Delta_t$ the time to reach equilibrium. Using non-linear least squares regressions (R language for statistical computing version 3.1.0 function nls(), Team, 2013) to fit the curve to the respective simulation output. Figure 2 shows a typical example.

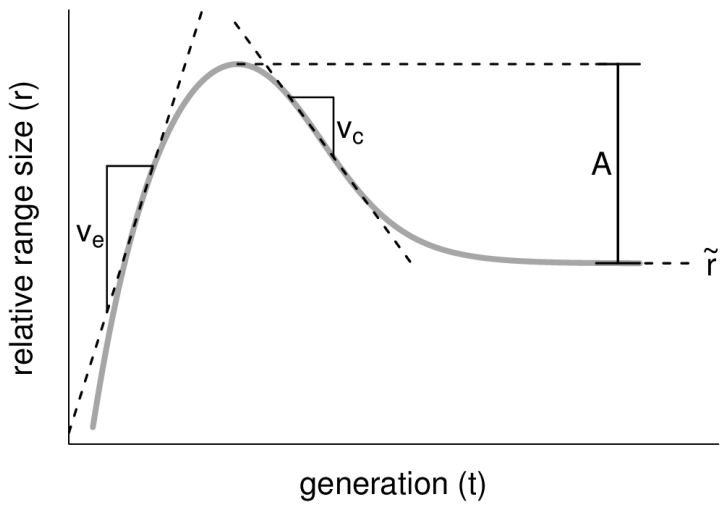


Figure 2: A sketch of the for elasticity typical relationship between relative range border position and time. The curve was created by using eq. 2 with the following parameters: $v_e = 0.0015$, $v_c = 0.0004$, $\Delta_t = 2000$, $\tilde{r} = 0.35$). The meaning of the four parameters used in the analysis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

# Results

Elasticity was only detected in one specific gradient type: gradients in dispersal mortality, i.e. patch isolation. All other gradients ($K$, $\lambda$, $\sigma$, $\epsilon$) did not lead to range border elasticity (Supplementary material Appendix 1, Fig. A1 - A4). Importantly, for gradient in dispersal mortality (i.e. patch isolation) we find an increasing degree of

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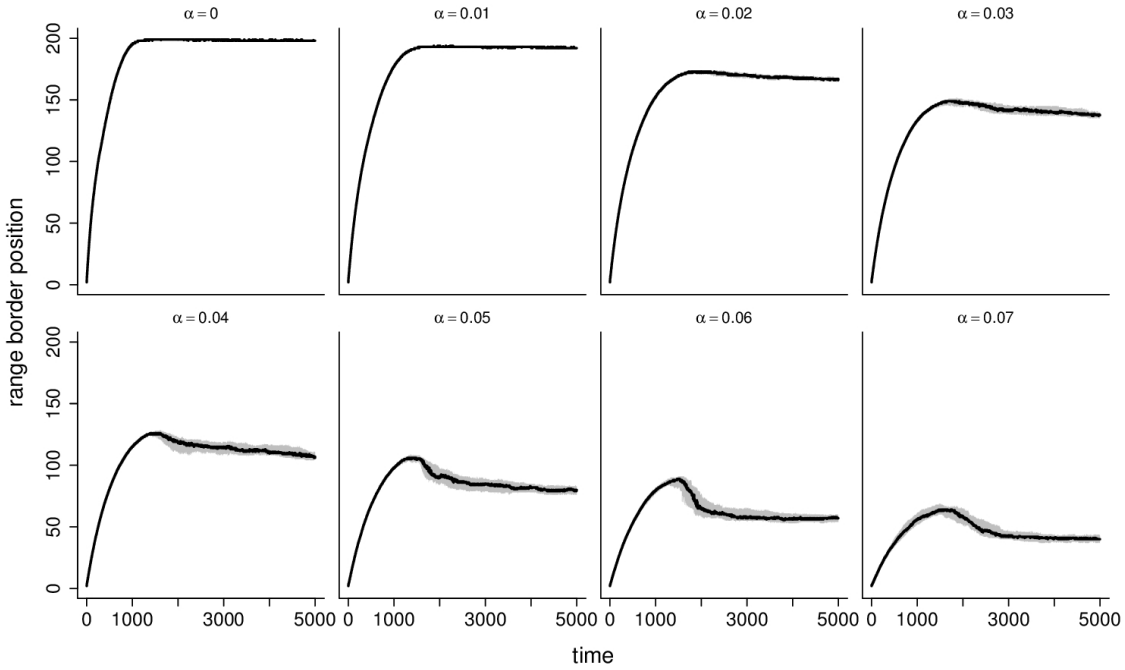


Figure 3: Range border position as a function of simulation time for a gradient in dispersal mortality ($\mu$). Allee effect strength increases from the top left to the bottom right panel. For parameter values see main text. The black lines show the median values of 50 replicate simulations, the shaded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

elasticity with increasing Allee effect strength (Fig. 3). For values of $\alpha$ exceeding 0.07, the entire spatially structured population went extinct. It is also important to note that we did find elastic ranges for our mixed gradient - scenario, invoking declining patch size and increasing patch isolation (Supplementary material Appendix 1, Fig. A5).

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

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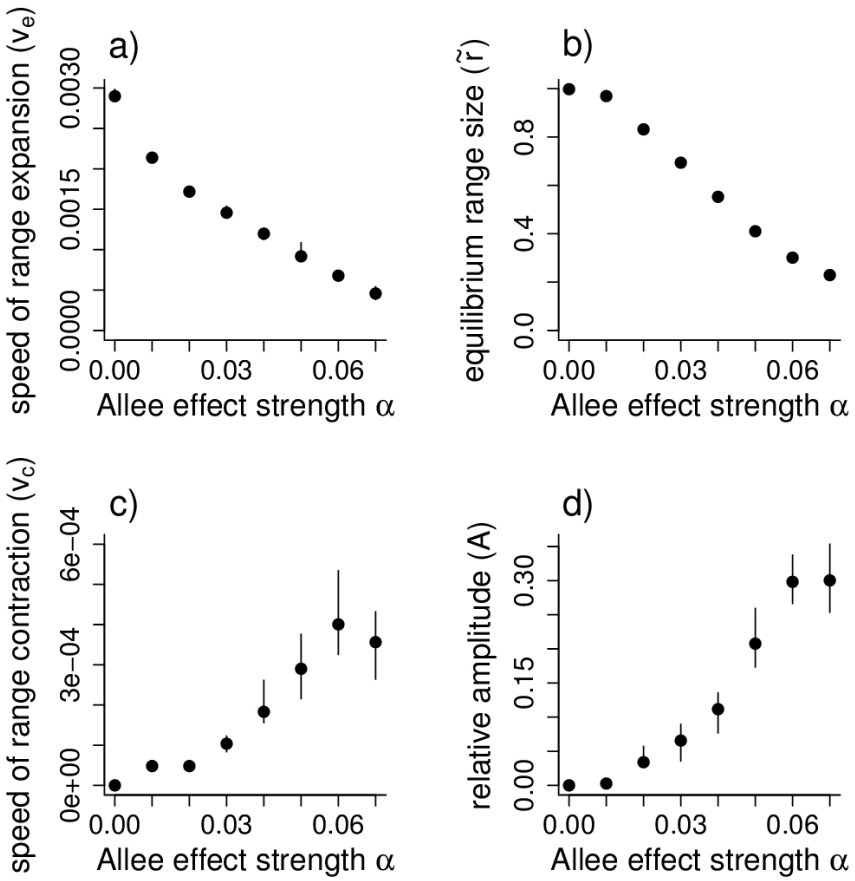


Figure 4: Results of the quanitative analysis of elasticity depending on Allee effect strength. Shown are (a) the speed of range expansion, (b) the relative range size, (c) the speed of range contraction and (d) the relative amplitude of the elastic range effect. Shown are median values of 50 replicate simulations, error bars denote 25%- and 75%-quantiles.

# Discussion

Our results show that Allee effects are a necessary prerequisite for ranges to show elastic behavior. The selective regime at the range margin changes, as the expansion period goes on – during range expansion benefits of lowered competition and spatial selection lead to increased dispersal, in equilibrium the source/sink-structure at the margin, caused by an Allee effect, leads to decreasing dispersal and thus range contraction.

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

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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), summarized 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. 1). Note that the findings of Kubisch et al. (2010) were caused by an Allee effect, too. The authors modelled a species with sexual reproduction, thus implicitly assuming a mate-finding Allee effect (which is roughly comparable to values around $\alpha = 0.02$ in this study). 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 and 2) a (strong) Allee effect will lead to a subsequent contraction, i.e. elasticity (Fig 2,3 and Supplementary material Appendix 1, Fig. A1 A5). 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 increases. 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.

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) modelled 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

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range shift. Once climate change stopped the individuals continued to disperse further into unsuitable habitat due to a time lag resulting from the adaptation of the dispersal strategy. This results in a strong source/sink-situation, which leads to the evolution of lower dispersal and thus lets the distributional range contract. 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 the described phenomenon to occur.

### Conclusion

With this study we show that elastic ranges are caused by the interplay between selection for lower dispersal at the range margin 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. We suggest that in nature range contractions after expansions are most likely to occur in fragmentation gradient systems for species that reproduce sexually, show social behavior or are otherwise prone to suffer from an Allee effect.

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