



# Density-dependent dispersal and the formation of range borders

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Knowledge about the mechanisms of range formation is crucial for scientifically based species conservation strategies in the face of ongoing global climate change. In recent years an increasing amount of studies have focused on the influences of density-dependent dispersal on demographic and biogeographical patterns. However, it still remains unclear, to what extent and in what ways this strategy would affect the range formation of species. In order to fill this gap, we present a study using individual-based simulations of a species with discrete generations living along a dispersal mortality gradient. We compare the evolution of range sizes for species following density-dependent and density-independent emigration. Furthermore we assess the influence of environmental stochasticity and Allee effects on range formation, as both processes are known to play an important role for dispersal evolution. We find that density-dependent dispersal always results in much wider ranges than unconditional dispersal. Increasing environmental stochasticity, a predicted consequence of climate change, can remarkably expand the ranges of species living in such connectivity gradients if dispersal decisions are based on local population density. A strong Allee effect causes range contraction for both strategies, but the effect is considerably less dramatic under density-dependent compared to density-independent emigration. We strongly recommend accounting for these findings in future attempts to model species' range shifts due to climate change.

Understanding the processes, which lead to the formation of a species' geographical range, is of central interest in the light of shifting environmental conditions caused by global climate change or invasive species (Dukes and Mooney 1999, Holt and Keitt 2005, Anderson et al. 2009, Walther et al. 2009). This is especially true for the development of reasonable conservation management strategies (Phillips et al. 2008, Tobin et al. 2009).

Resulting range shifts are the outcome of interactions among habitat characteristics, demographics and dispersal. The latter is a key process in such shifts because it allows the colonization of empty, but suitable habitat patches. An important component of dispersal is emigration, which may involve behavioral decisions of individuals. It is well known that many species use information on patch quality for their decision to leave a patch or not (Enfjäll and Leimar 2005, Ronce 2007, Armsworth and Roughgarden 2008). Especially density-dependent emigration has been investigated empirically (Conradt et al. 2000, Enfjäll and Leimar 2005, Matthysen 2005) as well as theoretically (Travis et al. 1999, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Enfjäll and Leimar 2009). Yet, there is however little knowledge about the possible influences of density-dependent emigration on the formation of species' ranges (but see Travis et al. 2009). The intention of this study is to fill this gap. Specifically, we will compare the effect of density-independent and density-dependent emigration in populations exposed to an Allee effect.

Allee effects, i.e. reduced growth rates at low population densities, have long been underestimated in their importance for metapopulation dynamics, but are evident in many empirical studies (Kramer et al. 2009, Courchamp et al. 2010). In recent years, an increasing proportion of theoretical investigations focused on the impacts of Allee effects on biogeographical patterns (Dennis 2002, Travis and Dytham 2002, Kanarek and Webb 2010). Until now it is still unclear, to what extent Allee effects may shape species' ranges and influence their position in space (but see Keitt et al. 2001, Cabral and Schurr 2010).

Allee effects have two major influences on metapopulation dynamics and hence range formation: 1) established populations can go extinct more easily if they are reduced to low population densities by adverse environmental conditions and 2) Allee effects impede the colonization of empty habitat patches.

We expect that density-dependent emigration may affect both of these consequences: firstly, it should reduce the risk of extinction as population densities less frequently fall to such low levels that an Allee effect could influence the population's growth rate (Hovestadt and Poethke 2006); secondly, it might increase the chance of colonization by overcoming the Allee effect, because at low population densities no further emigration is expected.

Variability in population densities across space and time has been shown to intensify selection favoring dispersal, as the chance increases to migrate from high-density into low-density patches (Cadet et al. 2003, Poethke et al. 2007).

These effects might have strong influences on the range formation of species and will increase in their importance in the future. Usually the effect of climate change is described as an increase in annual mean temperature. However, an increasing number of authors suggest that the temporal variability of climatic conditions will increase as well, leading to a higher frequency of extreme climatic events (reviewed by Jentsch et al. 2007). This in turn will result in a higher spatial variability of population densities and hence should increase selection for dispersal (Poethke and Hovestadt 2002). We thus predict that the higher temporal stochasticity occurring during climate change will have considerable consequences for shifts of species' range borders along gradients.

Gradients in environmental conditions that ultimately prevent a species from further range expansion can be categorized according to their effect on growth rate (as modeled by Travis et al. 2005, Brooker et al. 2007), patch size (Bahn et al. 2006), extinction risk (Holt and Keitt 2000, Oborny et al. 2009), or patch connectivity (Virgos 2001, Körner 2007, Gastner et al. 2009). Clearly, certain changes in environmental attributes could have several such effects. For example, a gradient in habitat fragmentation typically affects connectivity and patch size. In this study, we are approaching this by implementing a gradient in dispersal mortality, which results in degrading connectivity along space. Such a reduction in connectivity is especially interesting, as it directly leads to a decrease in colonization probability, allowing extinction rates to exceed colonization rates and impede a further range expansion of the metapopulation.

In this paper we use well established individual-based simulation approaches to address a number of questions: 1) How does a gradient in dispersal mortality affect the establishment of a species' range limits, 2) how is the position of the range border affected by the emigration strategy (density-independent vs density-dependent) and a strong Allee effect and 3) how might increased environmental stochasticity, as it is predicted to accompany climate change, effect range formation for the given scenarios.

## The model

### Landscape and individuals

Here we use an individual-based model with discrete generations (for similar systems see Travis et al. 1999, Poethke and Hovestadt 2002, Kun and Scheuring 2006, Kubisch et al. 2010). The simulated world is spatially explicit, consisting of 100 columns (x-dimension) of 50 patches each (y-dimension), providing a total of 5000 habitat patches. Each column of patches is characterized by a specific value  $\mu_x$ , characterizing the dispersal mortality of emigrating individuals. This reflects the connectivity of patches in that region, i.e. habitat fragmentation. Gradients in patch size, per capita growth rate and extinction rate have been tested as well; these results are qualitatively described in the discussion.

Each individual carries different traits, i.e. its sex, its affiliation with a specific patch  $i$  and two alleles at a single diploid locus that encode the dispersal probability (either density-independent or density dependent, see below).

### Local population dynamics and Allee effect

Local population dynamics follow the discrete-time model of density-dependent growth provided by Hassell (1975). We extended this model by the implementation of a relative Allee effect, i.e. the effect depends on population density in relation to the patch's carrying capacity (see eq. 1c). Every female mates with one randomly chosen male. If no males are present no reproduction is possible. Afterwards every female gives birth to  $\Lambda$  offspring, where  $\Lambda$  is a random number drawn from a Poisson distribution with patch- and time-specific mean  $\bar{\Lambda}_{i,t}$ . For each patch and generation  $\bar{\Lambda}_{i,t}$  is drawn itself from a lognormal distribution with mean  $\lambda$  and standard deviation  $\sigma$ . The parameter  $\sigma$  simulates environmental stochasticity, which we assume to be spatially correlated with a radius of one single patch. At the end of each generation, every patch may go extinct with probability, independent of the current size of the population; thus represents the probability of external catastrophes. This ensures extinction and colonization processes necessary for the formation of a range border after initialization (see below). Newborn individuals survive with a certain density-dependent probability ( $s_{i,t}$ ):

$$S_{i,t} = \frac{b}{1 + a \cdot N_{i,t}}, \quad (1a)$$

$$\text{with } a = \frac{\lambda - 1}{K}, \quad (1b)$$

$$b = \frac{(N_{i,t}/K)^2}{(N_{i,t}/K)^2 + \alpha^2} \quad (1c)$$

with  $N_{i,t}$  representing population size  $N$  in patch  $i$  at generation  $t$  and  $K$  being the carrying capacity. The parameter  $\alpha$  describes the strength of the Allee effect. We assume a sigmoid increase in survival probability with the number of inhabitants in a patch (eq. 1c). Individuals in a population at density  $N_{i,t}/K = \alpha$  will thus have a decrease in their survival of 50% and so the population will have a decrease in growth rate of 50% as well. For standard values of the model parameters see Table 1.

Any offspring inherits one randomly chosen allele (that determines the probability to disperse) from each of its parents to allow for recombination. The alleles may mutate to form new alleles with a probability of  $m = 10^{-3}$  by adding a Gaussian distributed random number with mean 0 and a standard deviation of 0.2. The dispersal alleles were initialized with a uniform distribution between 0 and 0.2 for density-independent and between 0.8 and 1 for density-dependent emigration, both leading to approximately similar dispersal rates. Other start values were tested, but did not influence the outcome of the simulations.

Table 1. Model parameters with meanings and standard values.

Parameter	meaning	value
$K$	habitat capacity	100
$\lambda$	per capita growth rate	2
$\varepsilon$	extinction rate	0.05
$\delta_{\mu,x}$	steepness of the gradient	0.008
$\sigma$	environmental stochasticity	0–1
$\alpha$	Allee effect strength	0, 0.05

## Dispersal

After all individuals mature they emigrate with a certain emigration probability  $d$ , calculated differently for the two used scenarios: 1) for density-independent emigration (DIE),  $d$  is calculated as the arithmetic mean of the individual's two alleles  $a_1$  and  $a_2$ :

$$d = \frac{a_1 + a_2}{2} \quad (2)$$

2) for density-dependent emigration (DDE), the calculation of  $d$  follows the dispersal model provided by Poethke and Hovestadt (2002), i.e. no emigration at population densities below the dispersal threshold  $C_{th}$  and a nonlinear increase in emigration propensity for densities above this threshold:

$$d = \begin{cases} 0 & \text{for } \frac{N_{i,t}}{K} \leq C_{th} \\ 1 - \frac{C_{th} \cdot K}{N_{i,t}} & \text{for } \frac{N_{i,t}}{K} > C_{th} \end{cases} \quad (3)$$

with  $C_{th}$  being the individual's threshold density, calculated as in eq. 2.

Alternative models for density-dependent dispersal have also been suggested (Travis et al. 1999, Metz and Gyllenberg 2001, Kun and Scheuring 2006). However, Hovestadt et al. (2010) compare different approaches and demonstrate that models derived from first principles (Metz and Gyllenberg 2001, Poethke and Hovestadt 2002) are most appropriate to describe the relation between density and emigration rate. However, the model by Metz and Gyllenberg (2001) applies to populations with continuous reproduction while that by Poethke and Hovestadt (2002) has been developed for non-overlapping generations and hence is the model of choice for our simulations.

We assume nearest neighbor dispersal, i.e. the destination patch of an emigrating individual is randomly chosen from the eight habitat patches that surround the natal patch. We assume the world to form a tube along the x-dimension, i.e. if an individual leaves the world in the y-dimension on one side it will enter on the opposite side. Individuals crossing the world's limits along the x-dimension are reflected into the other direction. To test the robustness of our results for different border conditions, we also implemented absorbing world limits, i.e. all individuals crossing the limits die. However, this had hardly any influence on the model outcome.

As mentioned above, dispersal incurs a cost  $\mu$  calculated from the mortality values  $\mu_x$  assigned to the column of the natal and the destination patch. As we assume an environmental gradient, these column-specific values for the dispersal mortality change linearly along the x-dimension of the world, measuring from  $\mu_1 = 0.2$  to a maximum of  $\mu_{100} = 1$ . This can be translated into a steepness  $\delta_{\mu,x}$ , i.e. a change of  $\mu$  per  $x$ , of 0.008.

## Simulation experiments

In order to simulate the effects of increasing spatio-temporal variability in patch quality caused by global change, we tested several values for the magnitude of

environmental stochasticity  $\sigma \in \{0, 0.25, 0.5, 0.75, 1\}$ . We compared different outcomes of the model for all parameter combinations of the values for  $\sigma$  and two different values for  $\alpha$ , describing either no ( $\alpha = 0$ ) or a strong Allee effect ( $\alpha = 0.05$ ).

For all parameter combinations the simulations were repeated 20 times each. Table 1 summarizes all relevant model parameters, their meanings and the standard values used for the simulations.

All patches are initially occupied by  $K$  individuals. During the next 2000 generations the populations were allowed to adapt their dispersal traits to the local conditions until an equilibrium state was achieved and a stable range border had been formed. We determined the range border as the column that contained the outmost populated habitat patches. We tested additional range border criteria based on patch occupancy, but did not find any qualitative changes of our results. Emigration rates at range margins were calculated as the fraction of individuals emigrating from the five patch stripes immediately preceding the range border. We calculated range core emigration rates in the same way, but for the five habitat columns of the simulated landscape that lay behind the first two columns. These first two columns were omitted from the analysis to avoid taking edge effects into account.

To compare the frequency distributions of immigrants, we additionally counted the numbers of immigrants per patch and generation for patches either lying at the range margin or in the core over the last 50 generations.

For testing the robustness of our results we conducted a sensitivity analysis.

## Results

Our simulation results clearly demonstrate the importance of conditional dispersal for the formation of range borders. Density-dependent emigration consistently leads to wider ranges than density-independent dispersal (Fig. 1, 2).

More interestingly increasing environmental stochasticity has a negative effect on the range under DIE, whilst we observed range border expansion into areas with even higher dispersal mortality under DDE when  $\sigma$  increases (Fig. 2a). An Allee effect leads to a range contraction for both dispersal strategies, but the difference in the range size becomes increasingly pronounced with growing environmental stochasticity, i.e. under DDE the influence of an Allee effect is comparatively weaker (Fig. 2b).

As predicted by Cadet et al. (2003), in the range core both dispersal strategies show higher emigration probabilities with increasing environmental stochasticity. We observe lower emigration probabilities at the range margins than in the core (Fig. 3). In scenarios with DDE, higher environmental stochasticity correlates with a decrease in the emigration probabilities at the range border (Fig. 3c). However, for DIE they are increased (Fig. 3a). An Allee effect slightly decreases emigration at the border for both dispersal strategies, but does not qualitatively change the patterns (Fig. 3b, d).

Without environmental stochasticity ( $\sigma = 0$ ) both, the range core and the range margin, show little differences in the distribution of immigrant numbers per patch and

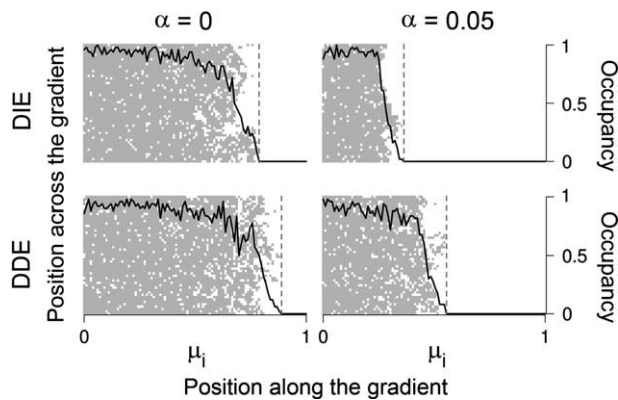


Figure 1. Snapshots of the metapopulation's occupancy at the end of in each case one exemplary simulation run (in equilibrium) for density-independent (DIE; top row) and density-dependent emigration (DDE; bottom row) and the two different intensities of the Allee effect (left column:  $\alpha=0$ ; right column:  $\alpha=0.05$ ). Grey squares denote occupied patches, white space unoccupied habitat. The gradient in dispersal mortality ( $\mu$ ) proceeds from left to right in each simulation (see x-axis). The black lines show the mean occupancy for every column of patches perpendicular to the gradient. The dashed lines indicate the location of the range border defined as the patch column containing the outmost occupied patches.  $\sigma=0.5$ .

generation between the two dispersal strategies, either with or without an Allee effect (Fig. 4, top row). However, slightly more events with large numbers of immigrants can be seen for DDE than for DIE. In scenarios with high environmental stochasticity ( $\sigma=1$ ; Fig. 4, bottom row), there are strong differences between the strategies. The distribution of immigrant numbers for DIE is slightly wider in the core, but does not change much at the range margin compared to the simulations with  $\sigma=0$ . However, the frequency distribution becomes strongly leptokurtic for DDE in the core and also in the margin area, especially under a strong Allee effect: there is a high frequency of patches receiving no immigrants, but there are also many events with very high numbers of immigrants.

The sensitivity analysis showed that under all tested model parameter values the wider ranges for DDE were robust to changing conditions (Appendix).

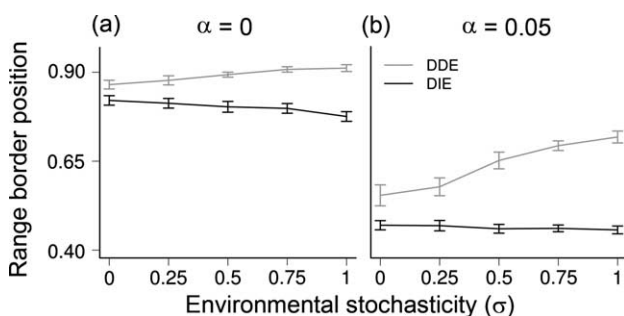


Figure 2. Influences of environmental stochasticity ( $\sigma$ ) and Allee effect (a:  $\alpha=0$ ; b:  $\alpha=0.05$ ) on the location of the range border, i.e. the value for dispersal mortality  $\mu_x$ , at which the range border is on average formed. Black lines: density-independent emigration, grey lines: density-dependent emigration. Shown are the arithmetic means of 20 replicates. Error bars denote standard deviation.

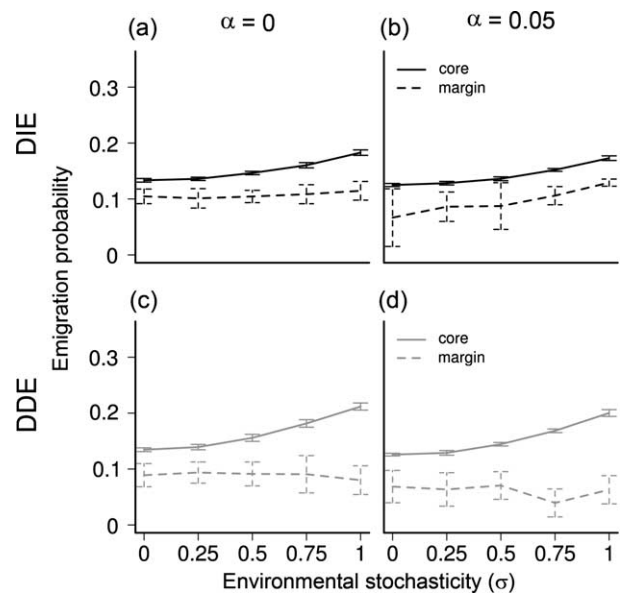


Figure 3. Emerging emigration probabilities at the range margin (dashed lines) and in the range core (solid lines) for all simulated scenarios (a, c:  $\alpha=0$ ; b, d:  $\alpha=0.05$ ). DIE: density-independent emigration (a, b), DDE: density-dependent emigration (c, d). For our definitions of core and margin see model description. Shown are the arithmetic means of 20 replicates. Error bars denote standard deviation.

## Discussion

The simulation experiments above presented demonstrate that accounting for the use of environmental information in dispersal decisions can have substantial consequences for the prediction of ranges established by species living in spatial fragmentation gradients. In all simulated scenarios, density-dependent emigration (DDE) leads to wider ranges than density-independent emigration (DIE).

It is well known that increasing environmental and demographic stochasticity, and hence, variation in population density between habitat patches, leads to selection for dispersal (Cadet et al. 2003, Poethke et al. 2003, 2007). In our results (Fig. 3) the emerging emigration rates in the range core increased accordingly with higher  $\sigma$ . This is due to the effect that more individuals will emigrate from high-density habitat patches that have a greater chance of arriving in less densely populated patches. However, the evolving emigration probabilities were higher in the range core than at the margin as a consequence of local adaptation to the dispersal mortality gradient, which is similar to the results of Dytham (2009).

More significantly, the simulations predict a range expansion with increasing  $\sigma$  under DDE, but range contraction under DIE. One reason for this difference can be found in the extinction risk, which is different between both dispersal strategies (Hovestadt and Poethke 2006): at low population densities, which are especially likely to occur at the range margin, individuals may still leave a sparsely populated patch under DIE, while this does not happen under DDE. At low densities populations have a higher chance of survival and growth in scenarios with DDE than with DIE. This is particularly relevant in the case of strong

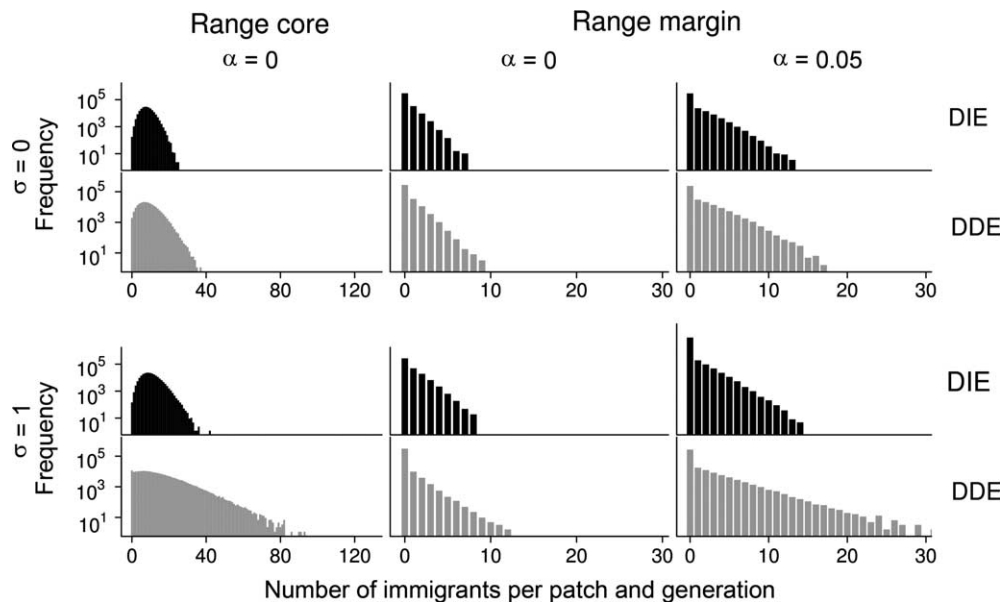


Figure 4. Influences of environmental stochasticity (top row:  $\sigma = 0$ ; bottom row:  $\sigma = 1$ ) and Allee effect strength (left and middle column:  $\alpha = 0$ ; right column:  $\alpha = 0.05$ ) on the frequency distributions of the number of immigrants per patch and generation arriving in the range core (left column) and range margin area (middle and right column). Grey bars: density-dependent emigration, black bars: density-independent emigration. There is no qualitative difference in the histograms for the range core when implementing the Allee effect, hence the corresponding results are not shown. The histograms are based on one representative simulation run. Note that the y-axis is scaled logarithmic and the different classes (x-axis) for range core and margin.

environmental fluctuations, as these induce great variability in population sizes. Furthermore we found strong differences in the distributions of the number of immigrants per patch and generation for the two dispersal strategies (Fig. 4). These show that – especially in the range core – higher values of  $\sigma$  lead to only a slightly higher variance in the distribution of immigrants under DIE (just because of the higher variance in population sizes), but to a strongly leptokurtic distribution under DDE. This is due to the fact that there are much more ‘bad’ years without any emigrants because of low population densities below the dispersal threshold. In addition, years of exceptional favourability may see events of ‘mass dispersal’ where emigration can occur in very high numbers. Hence an increase in  $\sigma$  leads to an increase in the number of events with many emigrants especially under DDE; this allows successful patch colonization even in regions with high dispersal mortality. This in turn allows for the formation of a wider range as less colonization events and less dispersal are necessary to maintain the borders of the metapopulation.

An Allee effect has negative effects on range expansion in both dispersal scenarios but obviously more in the DIE scenario. This is due to the fact that the Allee effect increases the extinction risk once a population has fallen to a low density. As already discussed this is more likely to happen if environmental stochasticity  $\sigma$  is high and more likely to occur under DIE than under DDE. Yet, more importantly, Allee effects influence the colonization probability of empty patches. In marginal populations with high dispersal mortality, immigrant numbers are generally low and successful colonizations occur rarely under the presence of an Allee effect. As a consequence, the benefit of dispersal is lower in these scenarios (Travis and Dytham 2002): if an individual is unlikely to successfully reproduce in an empty

patch then it is better for it to stay at home. In all scenarios, contractions in range sizes and lower emigration rates were observed, when we incorporated the Allee effect (Fig. 3, right panel). As the number of surviving emigrants decreases along the gradient, the Allee threshold can only be overcome closer to the range core, where dispersal mortality is relatively low.

More specifically an Allee effect leads to a sigmoid (and, as such, non-linear) increase of colonization probability with increasing numbers of immigrants in stochastic environments (Taylor and Hastings 2005). As marginal populations are only sparsely populated, this means that every additional immigrant leads to a disproportional increase in the probability of successful colonization (at low densities the progression of the colonization probability curve is exponential). This explains the increased discrepancy between range size for the two dispersal scenarios: the ‘boosted’ dispersal events caused by the leptokurtic distribution of the number of immigrants in the DDE-scenario can result in rare events of mass immigration that allow for the colonization of patches despite of the Allee effect.

From an emigrating individual’s perspective the more skewed distribution emerging in the DDE scenario implies that it will very probably be among a large group of immigrants upon arrival. This increases its probability to reproduce successfully in the new patch. For example in the simulations with  $\sigma = 1$  and  $\alpha = 0.05$  approximately 16.3% of the immigrants in the DDE scenario arrived in groups of more than five and hence had a good chance to overcome the Allee effect. In contrast <5.2% of the immigrants were in such large groups under DIE.

As the Allee effect fundamentally leads to a contraction of the range, the range border falls into regions where more

emigrants disperse successfully. Consequently the differences in the distributions of immigrants among DIE and DDE remain thus more pronounced. Hence, the colonization success is lower for DDE with an Allee effect than without, but increasingly higher than for DIE. The difference in the geographic range between species following either the non-informed (DIE) or the informed dispersal strategy (DDE) becomes larger.

Gradients in habitat fragmentation are common in nature (Körner 2007) and the effects of fragmentation have been well studied theoretically (Gastner et al. 2009) and empirically (Virgos 2001, Coulon et al. 2010, Magle et al. 2010). In this study we focussed on patch connectivity representing one aspect of habitat fragmentation. However, one can expect that increasing habitat fragmentation has further consequences, like lower growth rates, smaller patches or a higher frequency of environmental catastrophes. We ran additional simulations with gradients in these parameters (i.e.  $K$ ,  $\lambda$  and  $\varepsilon$ ) and the results showed that scenarios with DDE led to wider ranges than those with DIE in all environmental settings. However, the influence of the Allee effect on the difference between the two tested emigration strategies was smaller in gradients of  $K$  and  $\lambda$ , as in these scenarios the absolute population sizes were lower at the range margin and hence the diverging distributions of migrants were less pronounced. The gradient in extinction rate ( $\varepsilon$ ) nearly showed the same results like the one in dispersal mortality, as population sizes are still high at the range border.

Some authors have shown that Allee effects are expected to have strong influences on the geometry of species ranges. Keitt et al. (2001) as well as Gastner et al. (2010) conclude that the lower colonization probability caused by an Allee effect leads to a sharpened edge of the range and thus may stabilize dynamically fluctuating ranges. In this study we did not investigate range border sharpness, but we would hypothesize that density-dependent emigration could counteract this effect, as it increases the colonization efficiency of species. However, whether this assumption holds, is in need of further research.

The role of information-based dispersal, especially density-dependent emigration, for the formation of range borders has rarely been investigated before. We show that an Allee effect can lead to smaller ranges, but that it also increases the importance of acquiring and using current information about population density for dispersal decisions for an individual and range formation. Additionally, we show that increasing environmental stochasticity, as it is predicted to increase during climate change, might even lead to range expansions, if populations follow a density-dependent dispersal strategy. As individuals of many species are likely to incorporate information about their natal patch into their movement decisions (Matthysen 2005, Ronce 2007), these findings suggest that the appropriate choice of the dispersal model is of crucial importance when modeling the future distribution of species under global change.

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## Appendix

### Sensitivity analysis

We tested the robustness of the results presented in this paper by conducting a sensitivity analysis for all relevant model parameters. We changed every parameter by  $\pm 20\%$  and analyzed the difference between range border positions for DDE and DIE (i.e. position in the DIE – scenario subtracted from the position in the case of DDE) for  $\sigma = 1$  and either with or without an Allee effect. Sensitivity was calculated as the relative change of the named difference divided by the relative change of the according parameter. The results are shown in Table 2.

The results show that for all tested scenarios DDE led to wider ranges than DIE. However, the influences of the parameters were different. Habitat capacity proved to have a negative influence on the difference between range border positions (all sensitivity values are negative). This can be explained by the fact that higher population sizes lower the risk of demographic extinction and hence the benefit of DDE is less pronounced. Higher values for  $\lambda$  weaken the effect, too. As higher growth rates lead to faster population growth after colonization even in the case of DIE the demographic extinction risk is lowered and as a consequence the difference between the dispersal strategies is getting smaller. Because of the negative impact of these two parameters we hypothesized that extreme values might lead to the range difference vanishing. Therefore we also tested the sensitivity of the effect to such values by changing  $K$  to 1000 and found that the range difference was nearly not detectable without an Allee effect but was still present with an Allee effect included. We conclude that increasing  $K$  to large values aligns the predicted range borders for the two strategies. As the Allee effect in our model depends on the population density, the influence of big values for  $K$  is comparably small. Changing  $\lambda$  to 5 only led to a slightly positive difference between the range border positions for the two strategies, hence an alignment of the range borders occurs for large values of  $\lambda$ , too. A higher extinction risk clearly has a positive influence on the difference between range border positions. It increases the importance of colonizations and hence stresses the benefits of DDE.

The steepness of the gradient has hardly any influence on the results and is thus not of further importance.

Table 2. Results of the sensitivity analysis for a change of  $\pm 20\%$  of the relevant model parameters. Given is the difference in range border positions (DDE-DIE), i.e. positive values indicate wider ranges in the case of density-dependent emigration. The numbers in brackets denote the sensitivity of this difference for the given parameter. For a decrease of  $\lambda$  and  $\alpha = 0.05$  the populations in the DIE scenario went extinct.  $\sigma = 1$ . For detailed information see text.

		$\alpha = 0$	$\alpha = 0.05$
K	+	0.13 (–0.29)	0.25 (–0.16)
	–	0.18 (–1.76)	0.28 (–0.47)
$\lambda$	+	0.10 (–1.18)	0.23 (–0.47)
	–	0.20 (–2.35)	–
$\varepsilon$	+	0.14 ( $\pm 0$ )	0.46 (+4.06)
	–	0.13 (+0.29)	0.21 (+0.90)
$\delta_{\mu,x}$	+	0.13 (–0.04)	0.26 (+0.08)
	–	0.13 (+0.29)	0.26 ( $\pm 0$ )