Range border formation in a world with increasing climatic variance

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ABSTRACT

Questions: How will a change in climatic conditions characterized by an increase in the variance of environmental conditions affect the distribution of species along spatial environmental gradients? How does the specific type of gradient influence their response?

Features of the model: Spatially explicit individual-based simulation of a metapopulation. Logistic population growth and density-dependent emigration. Spatial gradients in habitat isolation, quality, and size.

Ranges of the key variables: Environmental stochasticity was modelled as a variation of net reproductive rate (λ). For a mean reproductive rate of $\lambda = 2$, the standard deviation (σ) was varied in the range of 0 to 3.

Conclusions: When the range margin was predominantly determined by a lack of colonizers, ranges initially expanded with increasing environmental fluctuations, but contracted again when these fluctuations became too strong ($\sigma > 1$). When extinction risk was more important for range formation, the initial expansion was damped or completely absent. When the climate changed too fast to allow for local adaptation of dispersal behaviour, the described patterns were less pronounced.

Keywords: climate change, density-dependent emigration, environmental gradient, environmental stochasticity, individual-based model, range formation, range shift.

INTRODUCTION

Climate change is expected to crucially influence the ranges of species and has been the focus of many recent biogeographical studies (Opdam and Wascher, 2004; Brooker *et al.*, 2007; Anderson *et al.*, 2009; Mustin *et al.*, 2009; Atkins and Travis, 2010). Mostly climate change is associated with a gradual temporal change in mean climatic conditions ['trends' in terms of Jentsch *et al.* (2007)]. However, consensus is emerging that increasing variance of conditions, not the change in mean conditions, will be of most importance for distributional patterns of

species (Easterling *et al.*, 2000; Jentsch *et al.*, 2007, 2009; van de Pol *et al.*, 2010). How such an increase in environmental fluctuations will ultimately influence the formation or change of range borders and their position in heterogeneous landscapes remains an unsolved question (but see Battisti *et al.*, 2006; Hochkirch and Damerau, 2009; Zimmermann *et al.*, 2009).

Many species exist in spatially structured populations, such as due to habitat fragmentation (Hanski and Gilpin, 1997). In such landscapes stable range borders are formed, where colonization of empty patches equals extinction of occupied ones along gradients that affect survival (Holt and Keitt, 2000; Guo *et al.*, 2005; Holt *et al.*, 2005). Consequently, it is either a too high risk of extinction or a lack of colonizers that impedes further spread of populations and dispersal is a key mechanism that affects both of these processes. If an increase in environmental fluctuations leads to an increase in local extinctions, it is assumed that increasing variance of conditions will lead to a contraction of range borders. However, dispersal is known to play a pivotal role in range formation processes and in the prediction of potential range shifts (Holt, 2003; Best *et al.*, 2007; Huntley *et al.*, 2010) and that environmental fluctuations strongly influence dispersal rates (Cadet *et al.*, 2003; Poethke *et al.*, 2007). Thus, increasing dispersal may counteract the effect of increased extinction.

It is clear that conditional dispersal (i.e. the use of information about the current environment) has strong consequences for the persistence and structure of metapopulations (Ims and Hjermann, 2001; Ronce, 2007; Armsworth, 2009). It has also been found empirically that conspecific population density is an important cue that triggers emigration (Conradt *et al.*, 2000; Enfjäll and Leimar, 2005). We recently investigated the consequences of such density-dependent dispersal for range border formation (Kubisch *et al.*, in press), and found that conditional emigration leads to wider ranges than unconditional dispersal. This effect becomes more pronounced with increasing environmental stochasticity caused by a shift in the distribution of emigrant numbers. When individuals of a population emigrate positively density-dependent, they will more likely not emigrate in 'bad' years with low population densities and leave their patches in higher numbers in 'good' years when growth rates are high and competition in their natal patches is increased. However, we did not investigate a further increase of this variance, especially in a comparison of different gradients that finally lead to range border formation.

In the present study, we wished to build on previous work by focusing on the effect of climatic variance on dispersal evolution and range border formation in different kinds of gradients. We used a spatially explicit (i.e. grid-based) individual-based modelling approach to simulate a metapopulation of a species with discrete (non-overlapping) generations living in a spatial gradient of environmental conditions. We applied gradients in patch isolation by increasing dispersal mortality, patch quality by decreasing per capita growth rate, or patch size by decreasing habitat capacity.

Our aims were to determine whether (i) higher environmental stochasticity leads to a consistent contraction of the range, and (ii) how the resulting patterns depend on the landscape (i.e. type of gradient) and its influences on range border formation.

THE MODEL

Landscape

We used an individual-based model of a metapopulation with discrete generations that has been used similarly in other theoretical studies (Travis *et al.*, 1999; Kun and Scheuring, 2006; Kubisch *et al.*,

2010). The model world was spatially explicit and consisted of $x \times y = 100 \times 50 = 5000$ habitat patches arranged on a rectangular grid. To investigate range border formation, we implemented habitat gradients by assigning to each column of patches (i.e. all patches that share one x-coordinate) certain values for important habitat characteristics and let these values change in the x-direction. We modelled an isolation gradient by increasing dispersal mortality from $\mu_{x=1} = 0.2$ to $\mu_{x=100} = 1$ (i.e. at the 'good' end of the gradient, 20% of all migrants survive, whereas at the other end of the gradient, no migrants survive). To simulate a patch quality gradient, per capita growth rate (see below) was decreased from $\lambda_{x=1} = 4$ to $\lambda_{x=100} = 0$. Patch size (the number of individuals that can reproduce successfully in the patch due to, for example, the amount of resources) was varied by decreasing local carrying capacity from $K_{x=1} = 100$ to $K_{x=100} = 1$. In every scenario, conditions at the 'bad' end of the gradient did not allow further spread of the metapopulation. For an illustration of the model world and range border formation, see Fig. 1.

Individuals

Each individual was characterized by its sex, its specific position in the model world and two alleles (c_1, c_2) at one locus, which determined its threshold density for emigration (see below). When an individual was born, its alleles were randomly inherited one from each parent and they mutated with a certain mutation probability ($m = 10^{-4}$) by adding a random number drawn from a normal distribution with mean 0 and standard deviation 0.2.

Population dynamics

Local population dynamics in each patch followed the discrete time model provided by Hassell (1975). After mating with one male chosen at random from the local population, every female gave birth to Λ offspring. Λ was a random number drawn from a Poisson distribution with patch- and time-specific mean $\overline{\Lambda}_{x,y,t}$. To simulate climatic fluctuations, the latter was drawn from a log-normal distribution with column-specific mean λ_x ($\lambda = 2$, if not considered as gradient) and standard deviation σ. Hence σ determined the magnitude of environmental stochasticity expressed in temporally fluctuating growth rates. Lastly, the survival probability for newborn individuals (s) was calculated as:

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

with $a = (\lambda_x - 1)/K_x$, where $N_{x,y,t}$ is population size N in the patch at coordinates x, y at generation t, and K_x is the carrying capacity of all habitat patches in column x of the world ($K = 100$ if not considered as gradient).

Dispersal

Offspring, which survived density-dependent population regulation, could emigrate from their natal patch. Emigration probability (d) was calculated according to the density-dependent dispersal model of Poethke and Hovestadt (2002):

$$d = \begin{cases} 0 & \text{for} \quad \dfrac{N_{x,y,t}}{K_x} \leq C_{th} \\[2em] 1 - \dfrac{C_{th} \cdot K_x}{N_{x,y,t}} & \text{for} \quad \dfrac{N_{x,y,t}}{K_x} > C_{th} \end{cases} \qquad (2)$$

where C_{th} represents the genetically determined threshold population density of every individual, calculated as the arithmetic mean of its two dispersal alleles ($C_{th} = (c_1 + c_2)/2$). Hence we assumed no emigration at all, if the population density lay below that threshold, and an asymptotic increase in emigration probability towards 1, if it lay above. This model
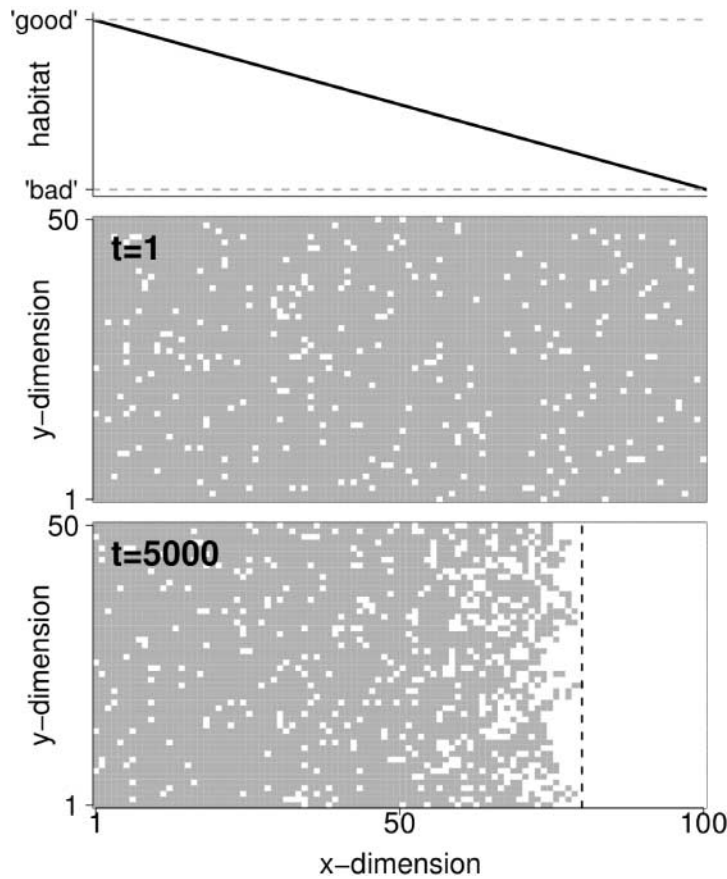
Fig. 1. Illustration of the simulation model. The upper panel shows schematically the progression of the habitat gradients, leading from 'good' conditions ($\mu_{x=1} = 0.2$, $\lambda_{x=1} = 4$ or $K_{x=1} = 100$ respectively) at the left end to 'bad' conditions not allowing metapopulation survival ($\mu_{x=100} = 1$, $\lambda_{x=100} = 0$ or $K_{x=100} = 1$ respectively) at the right end of the world. The middle panel shows a snapshot of a simulation (dispersal mortality gradient, $\sigma = 0$) after one generation. Grey squares denote occupied habitat patches, white space unoccupied habitat. At the end of the simulations (after 5000 generations), a stable range border was formed (lower panel; the dashed line shows the absolute range border position R).

is based on the marginal value theorem and has been shown to be most appropriate for modelling density-dependent dispersal in metapopulations with discrete generations (Hovestadt *et al.*, 2010).

Emigrating individuals died during the migration process with a certain dispersal mortality μ_x ($\mu = 0.2$ if not considered as gradient). We assumed nearest neighbour dispersal, i.e. the target patch for an emigrating individual was randomly drawn from the eight patches that surrounded its natal habitat.

To avoid edge effects, we modelled periodic boundary conditions in the *y*-direction, meaning that an individual that crossed the world's limits along the *y*-direction re-encountered it on the opposite side. When it would have left the world in the *x*-direction it was reflected back from the edge. The three columns of patches at the very ends of the world have thus been left out of the analysis. We tested absorbing border conditions as well, but these had no qualitative influence on our results.

Environmental catastrophes

Severe environmental fluctuations were modelled by implementing a random probability of local patch extinctions ($\varepsilon = 0.05$). This increased the rate of extinction and colonization events and facilitated range border formation after initialization of the simulations (see below).

Simulation experiments

We initialized the simulation experiments with all patches being occupied by K ($K = 100$ for all patches) individuals each (equal fractions of males and females). Alleles coding the dispersal behaviour of individuals (c_1, c_2) were initialized as uniform random numbers drawn from the interval $0 \leq c_i \leq 1$. Simulations were run for 5000 generations, which proved to be enough time for evolutionary adaptation to local conditions and hence the emergence of stable range borders. The position of the range border did not change for most scenarios after approximately 1000 generations.

Environmental stochasticity (σ) was varied in the range of $\sigma \in \{0, 0.5, 1, 1.2, 2, 2.5, 3\}$. For each parameter set we ran 25 independent replicate simulations, which was shown to be enough to determine the central tendency of the simulations (see standard deviations of the results in Figs. 2, 3).

We defined the range border R as that column (in the *x*-direction) of patches along the gradient where the outermost populated patch was located. Additional range border definitions (i.e. determining the range border as the column, where patch occupancy fell below 0.5 or 0.05, respectively) were tested, but had no qualitative influence on the results. The results of single simulation runs were the mean range border locations of the last 500 generations of simulation.

We also measured the relative range expansion r_{exp}, which we defined as the change of the range border location along the gradient for a certain increase of environmental stochasticity. Therefore, we divided the relative change of range border location Δ_R/R by the change in environmental stochasticity Δ_σ:

$$r_{\text{exp}} = \frac{\Delta_R/R}{\Delta_\sigma} \tag{3}$$

Positive values of r_{exp} indicate an expansion of range size for increasing environmental stochasticity, whereas negative values denote a contraction of the range if σ was increased by the given amount.

RESULTS AND DISCUSSION

Range border formation in the different gradients

In general, we see that high environmental stochasticity led to a strong contraction of the range for each simulated landscape (i.e. type of gradient; for the relative range border changes see Fig. 2, for the absolute locations see Figs. 3a–c). However, in the dispersal mortality gradient, lower amounts of environmental fluctuation ($\sigma < 1$) led to a wider range (Figs. 2a, 3a). A slight expansion of the range area was also evident for the growth rate gradient for low values of stochasticity, but to a considerably lesser degree (for $\sigma < 0.5$; Figs. 2b, 3b). In the gradient of carrying capacity, no wider ranges emerged; only range contraction was found for increasing environmental fluctuations (Figs. 2c, 3c).

The different reactions of the populations in these different types of gradients to an increase in environmental stochasticity may be explained by factors limiting distribution of a species in concert with the specific effects of density-dependent dispersal (Hovestadt *et al.*, 2010). Results show that in all tested gradients, the mean emigration rate in the range margin area (defined as the five columns of patches immediately preceding the absolute range border) increased with increasing environmental stochasticity, although the effect was more pronounced in gradients of habitat quality (λ) and patch size (K) (Figs. 3d–f).

It is well known that increasing environmental variation leads to selection for higher emigration rates, because it increases spatio-temporal variability of population density
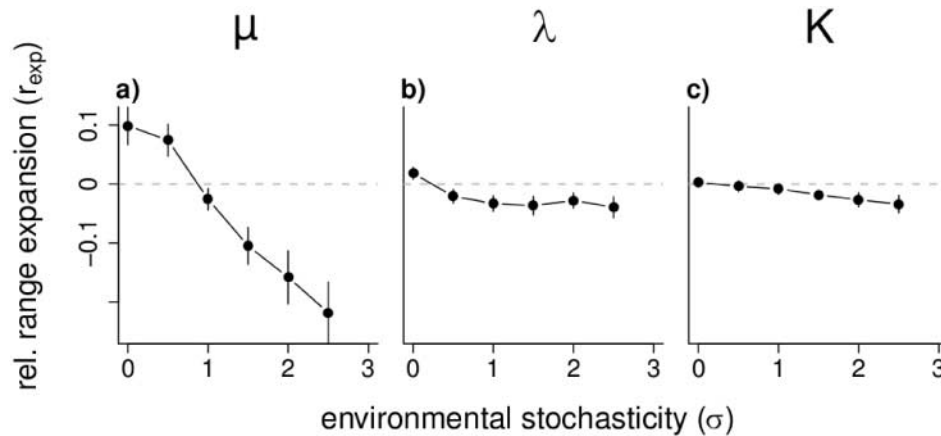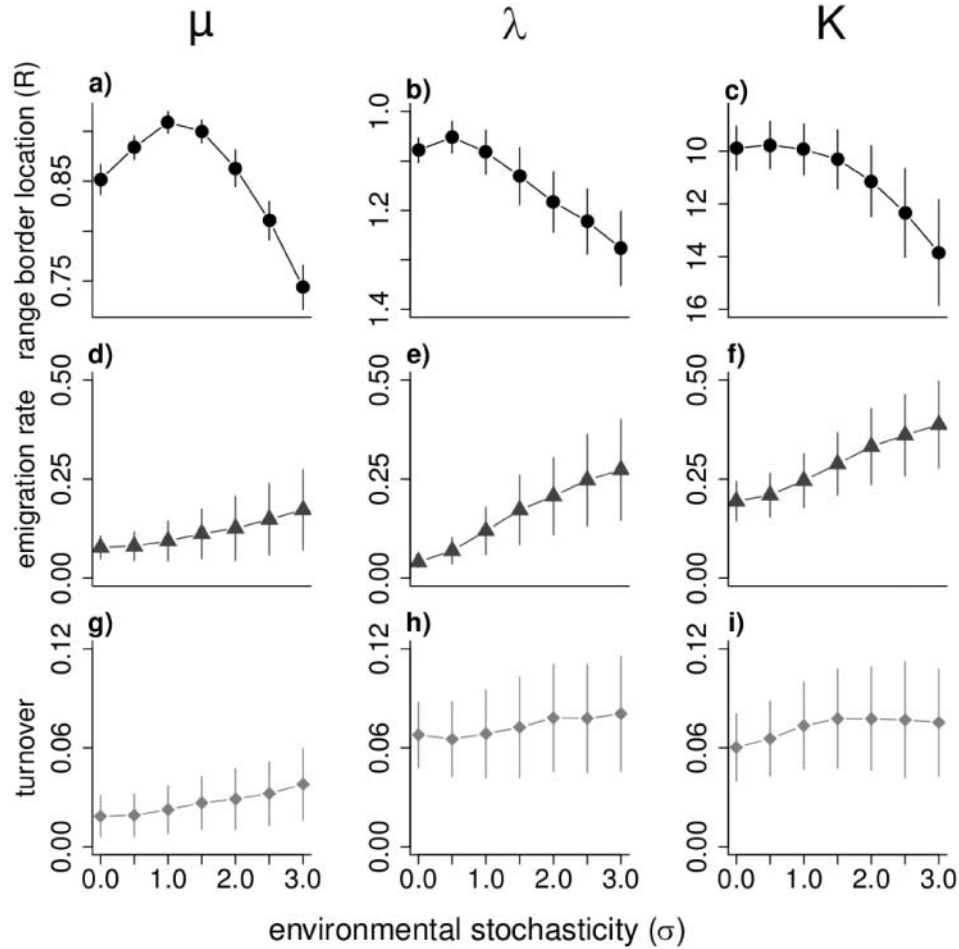

Fig. 2. Effects of increasing environmental stochasticity (σ) on range border formation in gradients of (a) dispersal mortality (μ_x), (b) per capita growth rate (λ_x), and (c) habitat capacity (K). The range border was defined as the x-position of the outermost populated patch and the relative range expansion (r_{exp}) describes the change of the border location for increasing σ at a given value by 0.5. Positive values indicate range expansion for higher σ, negative values range contraction. The means of 25 replicate simulations are shown; error bars denote standard deviation.

and thus the probability of dispersing from high- to low-density habitats (Cadet *et al.*, 2003; Poethke *et al.*, 2007). In the case of density-dependent dispersal in particular, increased temporal fluctuations of the environment result in a more skewed distribution of emigrants (Hovestadt *et al.*, 2010; Kubisch *et al.*, in press). In years with low growth rates, population densities are low and few individuals emigrate. In good years with high rates of growth, population densities are high and mass emigrations may occur. Together with the increased dispersal rates at the range margin, the increased probability of mass emigration induced the described initial range expansion in the isolation (μ) and habitat quality (λ) gradients, because it increased colonization probability. In the dispersal mortality gradient, it was the lack of colonizers that ultimately determined the limit of the range and hindered the further spread of the populations.

In the habitat quality (λ) gradient, low reproductive rates at the range border resulted in low mean population density. With density-dependent dispersal in particular, the low-density patches at the range border produced fewer emigrants and suffered from an increased risk of extinction (compare the higher patch turnover, i.e. the relative number of patch extinctions and colonizations per time step, between this scenario and the dispersal mortality gradient in Figs. 3g, h). Thus, emigration rates were lower in this gradient than in the gradient of dispersal costs. In the habitat capacity gradient, the range border was largely determined by the high demographic extinction risk in small patches (Hanski and Gilpin, 1997) (Fig. 3i), which can also be seen in the initially higher emigration rates (Fig. 3f). Further increasing variability in growth rates enhanced selection for dispersal, which resulted in an increase of patch recolonization, but it also increased the rate of patch extinction caused by increasing demographic stochasticity. Hence, no remarkable range expansion was observed in this scenario (Figs. 2c, 3c).

Poethke *et al.* (2003) pointed out the twofold effect of increasing environmental variation. They showed (Poethke *et al.*, 2003, figure 2) that increasing environmental variance lowers the risk of extinction due to the rescue effect caused by selection for higher emigration rates. However, increasing stochasticity also proved to heighten the population extinction risk. The same effect occurred in our present study: in each of the simulated landscapes, high environmental stochasticity strongly increased population-level extinction risk up to levels that could not be compensated by dispersal. Consequently, the ranges contracted in every gradient and the range margin formed in areas nearer to the range core, where dispersal mortality was lower, growth rates were higher or patches were bigger, all factors that lower the risk of extinction.

Our results clearly demonstrate that the effect of increased environmental stochasticity on the range of a species depends on the factors that limit its distribution and on the relative amount of environmental stochasticity already experienced at the range margin. When a further spread of the species is prevented by limited dispersal – either because high dispersal mortality selects against high emigration rates or because low spatio-temporal variability of population density (low environmental variance σ) does so – increased environmental variance may promote range expansion. These results support and help explain previous findings about expanding ranges after extremes of weather (Battisti *et al.*, 2006; Hochkirch and Damerau, 2009). However, when environmental fluctuations are already high and population sizes at the range margin are stochastic due to fluctuations in growth rate or small individual numbers, a further increase will likely result in increased extinction risk leading to a retraction of the range border into regions with more favourable conditions.

Fig. 3. Effects of increasing environmental stochasticity (σ) on the absolute range border location (R, a–c), emigration rates in the range margin area (d–f), as well as turnover rate at the range margin (g–i) for gradients in dispersal mortality (μ), per capita growth rate (λ), and carrying capacity (K). Range border was defined as that position in the gradient (expressed as the gradual changing parameter value) at which the outermost patch was populated (see Fig. 1). The range margin area contained the five columns preceding the range border (including the column of the range border). The arithmetic means of 25 replications are shown; error bars denote standard deviation.

Range border formation under non-equilibrium conditions

So far we have not considered the time scale of climate change. We have focused solely on equilibrium conditions and assumed that the change of environmental conditions is much slower than the evolution of adapted dispersal rates. However, populations need time to adapt to changing conditions. To account for this, we ran additional simulation experiments for the dispersal mortality gradient where we analysed different temporal gradients (i.e. different values of the annual increase $\Delta_{\sigma, t}$, of environmental fluctuations σ, Fig. 4).
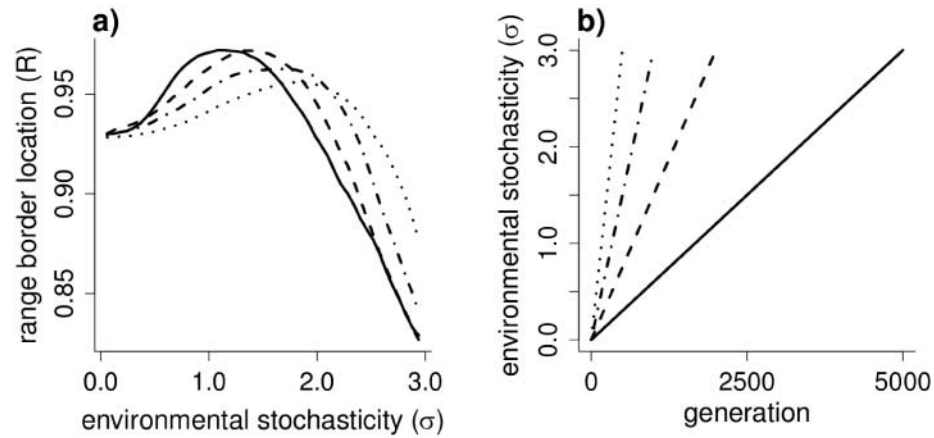
Fig. 4. To assess the influence of time on the results, we tested a temporal increase in environmental stochasticity during simulation time for the isolation gradient (dispersal mortality increasing in space). Shown are (a) the absolute range border position and (b) the corresponding temporal increase in environmental stochasticity (σ) over time. The number of time-steps for an increase of σ from 0 to 3 determined the speed of the change. Different types of line denote the corresponding changes in σ over 5000 (solid), 2000 (dashed), 1000 (dot-dashed), and 500 (dotted) generations. The arithmetic means of 25 replications are shown. To smooth the line, a moving average with a width of 10 data points was applied.

Results of this experiment suggest that for steep temporal gradients, the initial positive range expansion was delayed in its occurrence and damped in its extent. This was caused by the fact that evolution needs time – both the occurrence of beneficial mutations as well as their spread in the population due to natural selection needed time that was missing in these scenarios. The faster that environmental stochasticity increased (Fig. 4b; line types in Fig. 4a show the range border positions for the corresponding progressions of σ over time), the less that better-adapted dispersal phenotypes could occur by mutation and increase in frequency by selection in the time of increasing σ a certain amount. Hence the populations' ability to adapt to the new conditions was constrained and the effects of dispersal on the range border location were reduced. The time lag in the evolution of emigration rates persisted for further increasing values of environmental stochasticity. In this case, even the contraction of the range was mitigated, as dispersal rates were still quite high and allowed for persistence of the populations at higher values of dispersal mortality (i.e. deeper in the gradient) than in the quasi-equilibrium case of the slowest climate change. Interestingly, the mean population density at the margin was hardly influenced by the rate of increase (not shown), because in years with low growth rates the higher extinction probability was counteracted by the characteristics of density-dependent emigration [i.e. no emigration occurring at low densities (Hovestadt and Poethke, 2006)]. Of course in the long run, adaptation would take place and the range would contract.

CONCLUSIONS

In the present study, we show that increasing extreme environmental events (e.g. weather) can promote range expansion to a certain degree. However, this type of range expansion

would be restricted to cases where the range border of a metapopulation is predominantly determined by decreased colonization rates of patches (i.e. when dispersal at the margin is disfavoured). If, on the other hand, extinction risk at the range border is already high, either from the quality of the landscape (e.g. low patch quality or patch size) or by high environmental stochasticity, no range expansion is expected. Instead, the range would be expected to contract as the frequency of extreme events increases.

When accounting for non-equilibrium conditions, the speed of global change may determine the possibility of populations to adapt evolutionarily to the changing world. Hence the steepness of the temporal gradient has a strong influence on our findings. The faster the frequency of extreme events increases, the more delayed and less strong the range might react.

Our results underline the importance of understanding the factors that ultimately lead to the formation of range borders of species for the ability to draw appropriate predictions of future range shifts. The time scale of predicted changes also is of pivotal importance and should not be underestimated.

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