

EDITOR'S
CHOICE

Ecography 36: 873–882, 2013

doi: 10.1111/j.1600-0587.2012.00062.x

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Subject Editor: Janet Franklin. Accepted 3 November 2012

Predicting range shifts under global change: the balance between local adaptation and dispersal

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Bioclimate envelope models (BEMs) have often been criticized as being too simplistic due to e.g. not incorporating effects of biotic interactions or evolutionary adaptation. However, BEMs are widely applied and have proven to be often useful. Here we investigate, under which conditions evolution of dispersal, local adaptation or interspecific competition may be of minor importance for forecasting future range shifts. Therefore we use individual-based simulations of metapopulations under climate change living in spatial temperature gradients. Scenarios incorporate single-species systems or systems with competing species, respectively. Dispersal rate is evolving and adaptation to local conditions may also evolve in some scenarios. Results show that in single-species scenarios excluding evolutionary adaptation, species either follow optimal habitat conditions or go extinct if habitat connectivity is too low. These simulations are in close accordance to predictions from BEMs. Including evolutionary adaptation qualitatively changes these results. In the absence of competing species the species either completely invades the world or goes extinct. With competitors, results strongly depend on habitat fragmentation. For highly connected habitats the range border may shift as predicted by BEMs, for intermediate connectivity it will lag behind, while species will go extinct if fragmentation is too high. Our results indicate that (simple) BEMs may work well if habitats are well connected and species will not encounter many difficulties in dispersing to new sites. Selection in this case may promote evolution of even higher dispersal activities. We thus show that the presence of biotic interactions may be ignored for predictions of range shifts when high dispersal can be expected.

In the face of potential ecological and societal impacts of global climate change there is an increasing interest in forecasting future distributions of species, both in theory (Brooker et al. 2007, Mustin et al. 2009, Huntley et al. 2010) and practice (Jankowski et al. 2010, Thomas 2010).

It has been proposed that species distributions will change according to changing climatic conditions. Chen et al. (2011) have recently performed a meta-analysis regarding current range shifts of species. The authors could show that the individual species used for their analysis varied greatly in their rates of range shift. They concluded that many different factors have the potential to lead to lacks of species behind climate change, among these low mobility and multispecies interactions.

'Bioclimate envelope models' (BEMs; also referred to as species distribution models) have become standard tools to predict range shifts in response to environmental changes (for a review see Elith and Leathwick 2009). These models are based on statistical correlations between current (or past) species distributions and certain climate-related parameters, i.e. on the identification of a species' environmental niche. Based on the species-specific niche and

knowledge about future distributions of environmental conditions predictions of range shifts are inferred. However, BEMs have been criticized as too simplistic for not taking into account several aspects that are likely to influence the emergence of species' ranges (and their shift). Among these are the dispersal abilities of species, dispersal barriers and habitat fragmentation, the genetic variability of species and the potential for local adaptation, or the role of biotic interactions (Pearson and Dawson 2003, Hampe 2004, Dormann 2007, Beale et al. 2008, Atkins and Travis 2010, Lavergne et al. 2010).

Efforts have been taken to improve predictive models (Jeltsch et al. 2008, Thuiller et al. 2008, Anderson et al. 2009, Kearney and Porter 2009, Pagel and Schurr 2012) but to our knowledge it is still mostly ignored that the dispersal capacity and particularly the dispersal tendency of species is not a fixed trait but subject to potential evolutionary change. It has been shown that the dispersal behavior of species may quickly evolve in response to changed environmental conditions (Parmesan 2006, Hochkirch and Damerou 2009). Thus, it may be misleading to extrapolate from observed dispersal behavior under stable

conditions to the dispersal tendency (evolving) under changing conditions (Lavergne et al. 2010). However, it is not only the dispersal tendency that may show a fast evolutionary response to global change. There is increasing evidence that evolution of many different traits can occur much more rapidly than expected, making the historical discrimination between short (years to decades) ‘ecological’ and long (centuries to millennia) ‘evolutionary time-scales’ obsolete (Hairston et al. 2005, Reusch and Wood 2007). Rapid evolution may result in adaptation of populations to changing environmental conditions (Parmesan 2006, Pearman et al. 2008). Jump and Peñuelas (2005) have reviewed studies investigating the genetic diversity of species and potential evolutionary responses of plant populations under climate change. They conclude that in fragmented habitats changing climatic conditions could overwhelm populations as they could not track suitable conditions by dispersing, thus increasing the importance of possible evolutionary adaptation to the new conditions. Another very important factor for the formation of range borders are interactions with other species (Case and Taper 2000, Bridle and Vines 2007), but such interactions are largely ignored in BEMs (Beale et al. 2008, but see Boulangeat et al. 2012, Godsoe and Harmon 2012).

Regardless of these obvious limitations of most current BEMs many cases have been documented, in which these models performed well and produced results in good agreement with empirical data (Guisan and Thuiller 2005, Elith and Leathwick 2009). Thus, there must be environmental conditions, under which the described limitations are of minor importance for predicting the range formation of species. To investigate these conditions, we have developed an individual-based metapopulation model of either one or two competing species living along a large-scale temperature gradient and exposed to gradual climatic change. The species may evolutionarily adapt to local conditions and are thus allowed to shift their niches – an assumption justified by several studies (Prentis et al. 2008, Holt 2009, Holt and Barfield 2011). Yet, dispersal is the key process triggering the ability of species to track changing habitats. Our main focus thus lies on the balance between local adaptation and dispersal. Therefore we concentrate on the impact of habitat fragmentation, which is known to be of high importance for the evolution of both processes and is increasing due to anthropogenic influences (Bonte et al. 2012).

The model

Landscape and individuals

We are using a spatially explicit individual-based metapopulation model of a sexually reproducing species with discrete generations distributed along an environmental gradient. The model has already been successfully applied in theoretical studies mainly focused on dispersal evolution (Travis et al. 1999, Kubisch et al. 2010, Fronhofer et al. 2011) and was parameterized using empirical data (Poethke et al. 1996, Amler et al. 1999). In previous studies regarding

range formation we used a similar model to investigate the elasticity of ranges during expansion (Kubisch et al. 2010) or the influence of density-dependent emigration on range formation (Kubisch et al. 2011). However, in these studies no local adaptation to the habitat was included.

The simulated landscape consists of 125 columns (x -dimension) of 50 patches each (y -dimension), i.e. 6250 habitat patches in total. Every column of patches is characterized by its specific abiotic habitat conditions τ_x . For the sake of simplicity τ_x will be interpreted as ‘mean temperature’ throughout this manuscript. However, it may represent any other environmental condition that is systematically influenced by global change. This mean local temperature will be used for the determination of local adaptation of individuals. To simulate a large-scale habitat gradient, τ_x changed linearly from $\tau_{x=1} = 0$ to $\tau_{x=125} = 5$ along the x -dimension, i.e. by $\Delta\tau_x = 0.04$ when moving one step in x -direction.

Local populations (communities) are composed of individuals that are characterized by several traits: 1) the species it belongs to (in the two-species scenario), 2) its sex, 3) two alleles at one locus coding for the individual’s emigration probability, and 4) another two alleles at a locus coding for the individual’s ‘habitat preference’, i.e. the environmental conditions (temperature τ) under which the individual survives best.

Local population dynamics and survival of offspring

Local population dynamics follow the time-discrete Beverton–Holt model (Beverton and Holt 1957). We assume that females reproduce independent of their genotype, that the offspring born then compete (density-dependent survival) and that ultimately the offspring’s genotype affects further survival. In detail reproduction progresses in the following four steps.

1) Many populations, like of insects, exhibit strong annual fluctuations in growth rate. Hence, according to Poethke and Hovestadt (2002) we draw for each patch x, y at time t the females’ average fertility $\Lambda_{x,y,t}$ from a lognormal distribution with mean $2 \cdot \lambda$.

2) Each individual female in patch x, y then is assigned a random male from the same habitat patch (thus, males can potentially mate several times) and gives birth to a number of offspring drawn from a Poisson distribution with mean $\Lambda_{x,y,t}$.

3) Due to density-dependent competition offspring survive with probability s_1 , calculated as:

$$s_1 = \frac{1}{1 + \frac{\lambda - 1}{K} \cdot \sum_{i=1}^2 N_{i,x,y,t}}$$

Density-dependent survival s_1 is thus determined by the sum of individuals of the two species $N_{1,x,y,t}$ and $N_{2,x,y,t}$.

4) Finally, the surviving offspring experience a further density-independent mortality risk $1 - s_2$ that depends on the matching of their genetically determined optimal temperature (τ_{opt}) to the temperature conditions in patch x, y (τ_x) according to the following equation:

$$s_2 = \exp\left(-\frac{1}{2} \cdot \left(\frac{\tau_{opt} - \tau_x}{\eta}\right)^2\right)$$

In the case of the two-species scenario we assume symmetric competition for identical resources. This means that if both species are present in a habitat patch, they do not interfere with each other except for sharing the carrying capacity (i.e. for the calculation of density-dependent survival probability of offspring the total population size of both species is used). Hence, both populations grow according to the same conditions, but density-dependent individual survival (s_i) depends on the number of all individuals present, regardless of their species. Density-independent survival depends on adaptation to local conditions, i.e. on the difference between the genetically encoded optimal temperature τ_{opt} of an individual and local temperature conditions τ_x . η describes the niche width or ‘tolerance’ of both species. Thus we assume different environmental niches for all individuals. However, this allows for our simple approach of niche evolution. The niche of the whole species must be seen as the cumulative result of all individual niches. Note that consequently average population size could level values much lower than the theoretical K -value, if the population would consist mostly of maladapted individuals.

By using this approach we assume that density-dependent mortality ($1 - s_1$) acts before mortality due to maladaptation to local conditions ($1 - s_2$). It might also be reasonable to assume that the survival due to local adaptation of offspring is decreased in early phases of life, before density regulation through competition takes place. Hence we have also tested scenarios with local (mal)adaptation acting on the fecundity of females rather than on the survival probability of offspring. However, this did not qualitatively alter the results though the extinction risk of the metapopulation was slightly increased.

Dispersal

Individual surviving offspring disperse with probability d that is determined by their dispersal locus (see below). If an individual emigrates it will die with probability μ , which accounts for various costs that may be associated with dispersal in real populations, like fertility reduction or predation risk. We assume nearest-neighbor dispersal, i.e. successful dispersers settle in one of the eight surrounding habitat patches. To avoid edge effects along the gradient we wrap the landscape into a tube along the x -dimension. Hence, if an individual leaves the world in y -direction during dispersal, it will reenter the simulated world on the opposite side. However, if it leaves the world in the x -direction, it is lost from the simulation.

Genetics

As mentioned above, every individual carries two loci coding for its emigration probability and its habitat preference (optimum temperature), respectively. The phenotype of an individual is determined by calculating the arithmetic

means of the two corresponding alleles. Hence, dispersal probability d is given by $d = (l_{d,1} + l_{d,2})/2$ (with $l_{d,1}$ and $l_{d,2}$ giving the 2 ‘values’ of the two dispersal alleles) and optimal temperature τ_{opt} is calculated as $\tau_{opt} = (l_{a,1} + l_{a,2})/2$ (with $l_{a,1}$ and $l_{a,2}$ giving the ‘values’ of the two adaptation alleles, respectively). At each of the two loci (dispersal propensity and temperature preference) newborn individuals inherit randomly chosen corresponding alleles from each of their parents. During transition from one generation to the next an allele may mutate with a probability of $m = 10^{-4}$. Mutations are simulated by adding a random number drawn from a Gaussian distribution with mean 0 and standard deviation 0.2. In scenarios without evolutionary adaptation to environmental conditions only the dispersal alleles were allowed to mutate. To determine the influence of mutation rate on our results we tested a lower rate ($m = 10^{-5}$). This led to a lower degree of local adaptation and hence higher dispersal rates. However, the qualitative behavior of the system was equal in the resulting simulations, leading to the same conclusions. The sex of newborn individuals was chosen at random.

Simulation experiments

Simulations are initialized with a clear spatial separation of species. In the two-species scenario the colder half of the world (from $x = 1$ to $x = 62$) is exclusively occupied by the cold adapted species and the warmer half of the gradient (from $x = 63$ to $x = 125$) by the more warm adapted one. In the single-species scenarios we initialize simulations with the warm adapted species only. Its distribution is initially restricted to the warmer half of the gradient (from $x = 63$ to $x = 125$, assuming wrapped borders building a torus) while the colder half is kept free of individuals. At the beginning of simulations, dispersal alleles ($l_{d,i}$) are randomly drawn from the interval $0 < l_{d,i} < 1$. Local populations are initialized with optimally adapted individuals, i.e. preference alleles were initialized according to the local temperature τ_x .

Simulation experiments covered a time span of 3000 generations. To establish equilibrium conditions mean temperature τ_x in patches remained constant during the first 2000 generations. In the single species scenarios individuals were confined to stay in the warmer half of the gradient during this time. During the following 1000 generations global change is simulated by gradually increasing the temperature τ_x of every patch by a value of one in total ($\Delta\tau_t = 0.001$ per generation). We also tested more rapid ($\Delta\tau_t = 0.002$) or slower ($\Delta\tau_t = 0.0005$) changes in mean temperature but this did not change simulation results qualitatively. It is important to keep in mind that the numeral values of the temporal change are not comparable with real world predictions. The impact of climate change on the species in our simulations depends rather on the relation between the temporal increase of temperatures during climate change and the spatial temperature variation along (i.e. steepness of) the gradient.

To investigate the influence of habitat connectivity on range shifts we vary dispersal mortality from $\mu = 0$ to $\mu = 1$ in 101 equidistant steps. Hence, high dispersal

Table 1. Model parameters with meanings and standard values.

| Parameter | Meaning | Value |
|-------------------|-----------------------------------|-----------|
| K | habitat capacity | 100 |
| λ | per capita growth rate | 2 |
| σ | environmental stochasticity | 0.5 |
| m | mutation rate | 10^{-4} |
| $\Delta_{\tau,x}$ | slope of the temperature gradient | 0.04 |
| μ | dispersal mortality | 0–1 |
| η | niche width | 0.1; 0.5 |
| $\Delta_{\tau,t}$ | annual temperature increase | 0.001 |

mortality can be interpreted as low habitat connectivity, as dispersing individuals have a low probability of arriving in a new habitat patch. We performed simulations for species with a narrow niche ($\eta = 0.1$) and those with a wide niche ($\eta = 0.5$), equivalent to a decrease of survival probability of about $\Delta_{\mu} = 0.08$ (for the narrow niche) and $\Delta_{\mu} = 0.003$ (for the wide niche) when dispersing one patch away from the optimal habitat, respectively. As shallower gradients would have qualitatively the same effect as a wider niche, we did not vary the gradient's steepness.

Table 1 summarizes all relevant model parameters, their meanings and the standard values used for the simulations.

Analysis

At the end of the simulation we calculated the range border position R of a species i as that position in x -direction, where the fraction of occupied patches (I) fell below $I = 0.05$. In the two-species scenario this value was estimated independently for each species.

Alternative definitions (incidence below 0.5, 0.1, 0) did only marginally alter the results presented here. If species would exactly track the shifting temperature conditions (perfect envelope matching), the range border should follow changing temperature conditions and always lie in that landscape zone (in x -dimension) where temperature conditions are similar to those at the border before the onset of climate change (i.e. in generation 2000). However, as in the single species scenarios the range initially is restricted to the warm half of the gradient, the final range border will emerge at positions with slightly colder temperatures, according to the species' climatic niches (see below).

Results and discussion

Single species systems without creation of new optimum temperature alleles by mutation

To explore the dynamics of range borders in more detail we first restricted our simulation experiments to single-species systems. We initialized the simulations with one species occupying (and up to the moment global temperature increase sets in (generation 2000) restricted to) the warmer half of the world and kept the other half free of individuals. All cells were filled with individuals optimally adapted to local conditions. For further details see model section.

In a first set of simulations we did not allow mutations of the temperature trait while mutations at the dispersal

locus are allowed. Thus, the spectrum of temperature traits remains restricted to those genotypes initially introduced into the population. These single species scenarios yield only two principle outcomes. With low dispersal mortality (μ) the species initially increases its range slightly (indicated by the small positive deviation from the predicted range) and then follows the predicted shift (Fig. 1A, B). Alternatively, beyond a certain critical value for dispersal mortality ($\mu > 0.7$) the metapopulation completely collapses and the species goes extinct. Evidently, due to the inability of individuals to adapt to new temperature conditions by mutations, range expansion is constrained in this scenario although dispersal would potentially be sufficient. Thus the position of the range border is determined by the gradient and the species' niche limits. The initial increase in range depends on niche width (η) and is small for a narrow niche (Fig. 1A) and larger in the wide niche scenario (Fig. 1B). This shift is due to the fact that the species is – for the first 2000 generations – restricted to a range of optimal habitat conditions, while – due to its inherent temperature tolerance (niche width) the species could persist also in certain non-optimal (but initially inaccessible) habitat further down the gradient. The moment this restriction is released (in generation 2001) these new habitats are quickly colonized. Apart from this artifact and as long as dispersal cost (μ) does allow sufficient dispersal rates, the range shift observed during the time span with climate change is indeed fully congruent with predictions from envelope models. Note that in our scenario after complete range filling the marginal populations might partially be sink populations. Pagel and Schurr (2012) refer to this fact and conclude that BEMs tend to overestimate the ecological niches of species due to the accidental incorporation of sink habitats. Certainly, this scenario of incomplete range filling is rather artificial, but it is necessary to understand the following scenarios and their implications.

In our model, without the creation of 'new' genotypes by mutation dispersal is the only possibility of populations to track the changing environmental conditions during climate change. As long as gene flow is sufficiently large, the population can in fact track changing conditions infinitely. Yet, if dispersal mortality (μ) becomes too high two reasons prevent tracking of optimal adequate conditions: First, high dispersal mortality eliminates a large fraction of dispersers and second, it selects against dispersal thus limiting the number of emigrants. Both factors combined ultimately prevent gene flow of adapted types at a rate large enough to track environmental change and hence average fitness decreases (maladaptation increases) until the whole metapopulation finally collapses (see Fig. 2 for metapopulation sizes). Note that this process takes some time depending on the strength of gene flow. In the long run we would thus expect that for all cases where the species was not able to fully track climate change anymore ($R > p$) populations would ultimately collapse, creating a sharp transition between either complete envelope matching or complete extinction. The critical cost of dispersal (μ) that allows metapopulation survival is approximately identical for the narrow and the wide niche scenario.

In summary, in the single-species system without mutations of the temperature trait the prediction of the climate

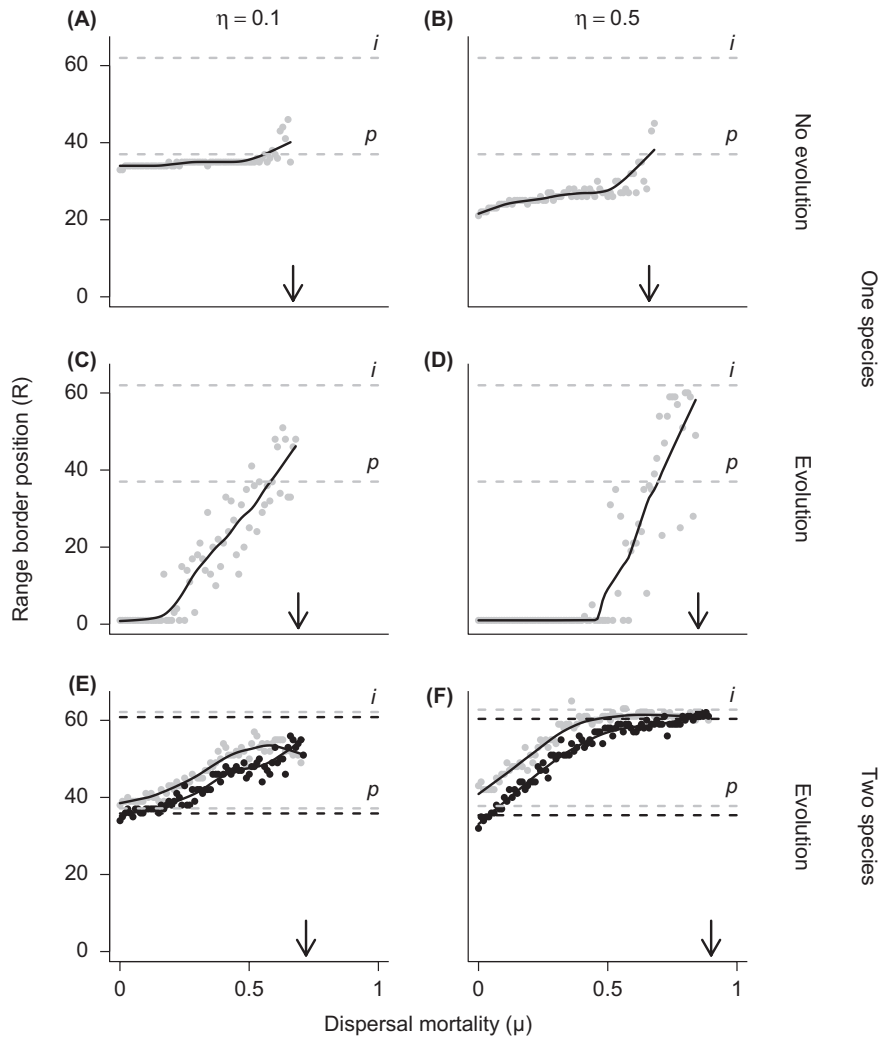


Figure 1. Influence of dispersal mortality on the realized range border position R at the end of the simulated period ($t = 3000$). Left panels show results of narrow ($\eta = 0.1$) and right panels of wide niches ($\eta = 0.5$), respectively. (A, B) Single-species scenarios without evolutionary adaptation; (C, D) single-species scenario with evolutionary adaptation; (E, F) two-species scenario with evolutionary adaptation to temperature change. Light grey dots resemble range border positions for the 'warm-adapted', dark grey dots for the 'cold-adapted' species, respectively. Horizontal lines denote initial range border position (i) and BEM prediction (p). Shown are the results of 101 simulation runs for different dispersal mortalities ($\mu = 0, 0.01, 0.02, \dots, 1.0$). Arrows above the x-axis indicate the critical dispersal mortality, above which the system (ultimately) goes extinct; corresponding R -values were thus omitted. Lines were fitted using the lowess algorithm provided by Cleveland (1981).

envelope basically holds as long as dispersal remains sufficiently high; this will be the case as long as no strong dispersal barriers exist and costs of dispersal are not too high.

Single species systems with creation of new optimum temperature alleles by mutation

Up to a certain dispersal risk the realized range shift in the single-species scenario described above matched the bioclimate envelope prediction, i.e. the species manages to track the change in environmental conditions by dispersal. However, so far we ignored the possible emergence of new genotypes (resulting in better adapted phenotypes) by mutation at the locus determining temperature preference. However, it is likely and indicated by empirical evidence that new and better-adapted genotypes could also emerge by

mutation (Thompson 1998, Reznick and Ghalambor 2001). In fact, negating this possibility may appear highly implausible if we on the other hand assume that dispersal traits may evolve in response to changing habitat conditions; a proposition supported by considerable evidence (Hill et al. 1999, Parmesan 2006, Phillips et al. 2010). Hence we performed a second set of simulation experiments allowing the alleles coding for the optimal temperature to mutate, too (see model section), i.e. we consider a scenario where the dispersal trait and habitat adaptation can jointly evolve due to mutation.

Results for these simulations considerably differ from those of the previous one. For highly connected patches (low μ) the species now simply invades the whole gradient. It thus manages to evolve – in spite of the ongoing temperature increase – even cooler adapted individuals at the rapidly advancing front (but also 'hotter adapted' types at the

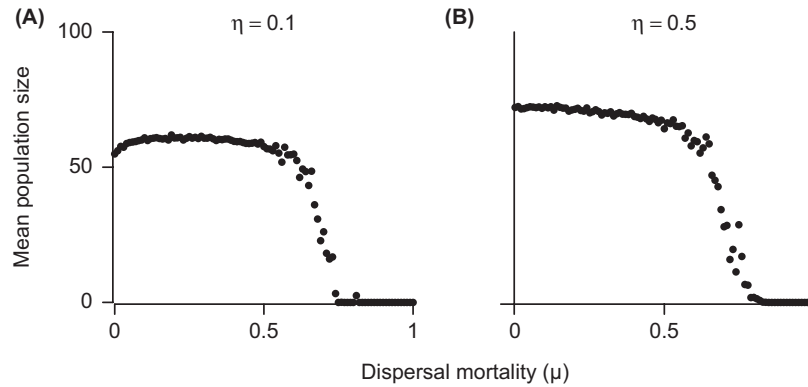


Figure 2. Mean population sizes for the single-species scenario without mutations of local adaptation. Shown are the averaged population sizes of all occupied patches for every simulation (Fig. 1). (A) Narrow niche ($\eta = 0.1$), (B) wide niche ($\eta = 0.5$).

‘warm end’ of the initial range). This implies that evolutionary change is more rapid than environmental change, i.e. local adaptation to changing conditions (either by climate change or immigration into habitat beyond the species’ current niche) progresses faster than the conditions change during climate change. Evolutionary adaptation explains the large range expansion that is only restricted by the limits of the simulated landscape (Fig. 1C, D). For intermediate dispersal cost species expand their range still faster than predicted ($R < p$). However, range expansion is slower and the landscape is not completely filled. Nevertheless, given enough time these metapopulations would invade the whole simulated landscape, too. Finally, for the scenario including wide niches ($\eta = 0.5$) survival of metapopulations becomes possible over a wider range of dispersal mortality (compare Fig. 1B–D) while the system collapses at about the same dispersal mortality (μ) than in the previous scenario if the niche is narrow (compare Fig. 1A to C). Regardless of adaptation to local conditions metapopulations necessarily go extinct for two main reasons when dispersal mortality gets too high. First, due to competition among kin always a certain percentage of individuals will emigrate and thus eventually die (Hamilton and May 1977). Second, in the case that no immigrants arrive in local populations, every population will go extinct in the long run due to demographic stochasticity, resulting in a phenomenon also referred to as ‘evolutionary suicide’ (Gyllenberg et al. 2002). However, niche width affects the ability to persist locally and selection against non-optimal genes, respectively against being in the wrong habitat, becomes weaker as the niche becomes wider (the tolerance becomes larger). This may allow adaptation to changing conditions even under circumstances where gene flow becomes very weak and thus allows persistence even in very isolated habitats.

With mutational change of habitat (temperature) preference, the envelope approach thus becomes inappropriate for single species systems. No matter whether we introduce climate change or not, without dispersal barriers evolutionary adaptation would principally allow that a species extends its range along the whole gradient. However, if adaptability or dispersal are insufficient to match the rate of changing habitat conditions, the species will go extinct anywhere.

The results of the previous simulations suggest that species could be expected to expand their ranges over the

whole world. Similar results have been provided by Kirkpatrick and Barton (1997). By using an analytical model the authors showed that – based on several parameter combinations – the simulated species could either go extinct, fill up to its full potential range or exhibit limited distributions based on maladaptation caused by gene flow between populations. The idea of limited ranges as a consequence of gene flow from central to peripheral populations has attracted much attention in the literature (Holt and Gomulkiewicz 1997, Bolnick et al. 2008), although it has also been argued that a lack of gene flow might hamper range expansion by not providing enough genetic diversity to allow for adaptation to new conditions (Kawecki 2008). For range limit emergence because of this ‘migration load’, i.e. gene flow causing maladaptation, high rates of dispersal are necessary. However, in our simulations emigration rates do not evolve to levels high enough for maladaptation through gene flow. Hence, in this setting range limitation through gene flow is impossible. As dispersal is known to be highly plastic and evolvable (Ronce 2007), it is fundamentally questionable, whether this hypothesis is likely to be true for many systems. Recently, Schiffrers et al. (in press) have investigated the interactions between habitat heterogeneity, gene flow and dispersal evolution for the survival of populations under climate change. They found that gene flow and habitat heterogeneity may effectively decrease dispersal, thus reducing the probability for rescuing populations close to extinction.

Despite of that, numerous additional mechanisms for the formation of range borders have been described (Holt et al. 2005, Sexton et al. 2009). Such mechanisms include environmental gradients in colonization or extinction rate, patch size or growth rate, but also Allee effects. Although these landscapes and conditions may easily prevent species from infinite range expansion, their influences cannot be directly compared to the approach we follow in this study, as we here focus on the evolution of species’ niches. As such, the conclusions we draw from the single-species scenario do not hold for all possible scenarios of range limitation.

It is often argued that physiological constraints lead to range limitation in a scenario of local adaptation. Nevertheless, when thinking about evolutionary time scales, the picture is different. Given large enough time scales it is reasonable that a single species – when introduced

into an empty world – would generally be able to expand its range globally. Evidently this reasoning only applies as long as we consider space that – along an environmental gradient – holds critical resources required by a specific guild or functional group of rather similar species. The associated genetic diversification would, however, lead to speciation processes and thus rather result in a set of interspecific range borders. This idea is also supported by results from Doebeli and Dieckmann (2003), who could show that evolutionary branching equivalent to sympatric speciation is easily possible along environmental gradients.

Range shifts in a two species system

The invasion of the whole world in the above scenario was only possible because we deliberately imposed and maintained the presence of ‘empty space’ before the onset of climate change, otherwise such empty habitat would not exist. However, habitats and landscapes are rarely free of other species and interactions with competitors, predators or parasites are important mechanisms that shape the distribution of species (Gaston 2009, Price and Kirkpatrick 2009). We thus introduced a second, competing species into the simulations, locally adapted to the cooler half of the gradient, but otherwise identical to the first species (for details see model section).

In the two-species scenario we neither found the initial range expansion nor any range shift faster than predicted by

the envelope model. Instead, with increasing dispersal cost (μ) we witness an increasing lag in the shift of the range border of the ‘warm adapted’ species compared to BEM predictions (Fig. 1E, F). This corresponds to a gradual shift from tracking changing environmental conditions by dispersal to local adaptation due to mutation. For very low dispersal costs ($\mu \rightarrow 0$) the realized range shift nearly matches the prediction of the climate envelope because preadapted individuals of the generally ‘warm adapted’ species move forward according to the progressing climate change and replace the (increasingly) poorly adapted second species. However, as dispersal mortality becomes larger and correspondingly gene flow becomes lower, the competition with better-adapted immigrants decreases and the retreating species increasingly gets the time and chance to adapt to changing conditions as adequate mutants emerge. Consequently, the shift of the range border increasingly lags behind predictions (Fig. 3A, B showing the balance between these two processes). The lag is more pronounced in the scenario with wider niche for the reasons already outlined above – if individuals are generally more tolerant to a deviation from ideal conditions, genetic diversity will be larger locally, providing a larger pool of variants from which better adapted individuals can be selected as environmental change progresses. Further, the selective pressure on dispersal induced by the change in environmental conditions is weaker for the tolerant species (having a wider niche is similar in effect to a slower change in environmental conditions) and evolved dispersal is consequently lower in the scenario assuming a

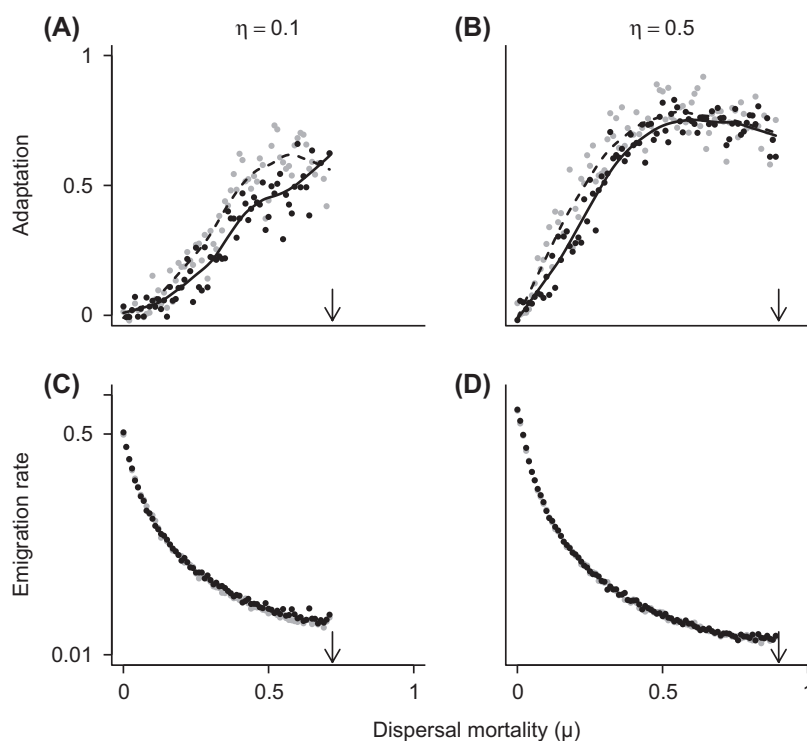


Figure 3. Evolved adaptation (A, B) and emigration rates (C, D) for the two-species scenario. (A, B) Shown is the difference between the individuals’ mean optimal temperatures at the beginning and end of climate change, normalized to the temperature increase (see main text). The higher the values the more the species’ adaptation deviated from the temperature at the predicted range margin. (C, D) Shown are the arithmetic means of emigration rates for both species at the end of the simulations. Dark grey dots: warm-adapted species, light grey dots: cold-adapted species. (A) Narrow niche width ($\eta = 0.1$), (B) wide niche width ($\eta = 0.5$). Lines were fitted using the lowess-algorithm provided by Cleveland (1981).

wide niche (Fig. 3C, D). The critical value of μ , at which the system collapses is, however, not affected by the introduction of a second species (compare Fig. 1E, F and Fig. 2C, D) and there is indeed no reason why it should be so. Despite the fact that the rate of range shift is predominantly determined by the interaction between the species, the extinction probability for the system as a whole depends only on the ability to cope with the changing conditions. As long as species do only differ in their temperature preference this does, however, not depend on the number of species in the system.

Conclusions: predicting future range shifts of species

With this study we aimed at identifying environmental conditions, under which certain shortcomings of classical BEMs are of minor importance. Our results show that predictions of BEMs should be most accurate, when the habitat is well connected and thus high dispersal is likely to evolve (Fig. 1E, F and Fig. 3C, D). Hence, based on these results we would expect an important role of local adaptation to changing temperatures for species living in highly fragmented habitats, like e.g. islands. In these cases dispersal is strongly selected against and is thus an unlikely source of new genotypes. It might, however, be possible that BEMs are even capable to accurately predict range shifts of species with initially low dispersal potential living in fragmented habitats. The reason for this could be an increase in dispersal itself due to the effects of climate change, either directly by physiological reactions to changed habitat conditions or by the evolution of dispersiveness during periods of expansion (Kubisch et al. 2010, Phillips et al. 2010).

The amount of range shift is thus always dependent on the balance between tracking the changing conditions by dispersal (gene flow) or adapting to them due to rapid evolution (mutation). In any specific case this balance will be affected by different factors like the rate of climatic change, the connectivity of habitats, the steepness of the habitat gradient, the tolerance (niche width) of a species to temperature change (or habitat changes associated with it), genetic diversity, mutation rate and so forth.

A lot of studies base their predictions on observations of single species distributions (Bakkenes et al. 2002, Montoya et al. 2009, Adams-Hosking et al. 2011). Yet as soon as we allow adaptation of species to changing conditions by mutation, the single species scenario becomes as such meaningless. At this point it is important to keep in mind that the genetic structure used in our simulations is fairly simple. It has for example been shown that genetic correlations between multiple quantitative traits may severely affect species' range shifts in changing climate, being impacted by spatial environmental variation (Duputié et al. 2012). Nevertheless, we took this approach for reasons of simplicity and are convinced that this issue does not touch the general conclusions we draw concerning the conditions under which biotic interactions are necessary to be included to improve BEM predictions.

Yet the world is typically not empty but occupied by other, competing species. When generating predictions concerning the response to climate change we thus would

expect that the incorporation of interactions between species is crucial. Several authors have already stressed the importance of biotic interactions for predicting future distributions and attempts have been made to integrate these into BEMs (Hampe 2004, Araújo and Luoto 2007, Dormann 2007, Boulangeat et al. 2012, Godsoe and Harmon 2012), but a mechanistic model integrating interactions was still lacking. Our results demonstrate that the presence of competition, just one of the types of biotic interactions, can be ignored when the dispersal abilities of a focal species are known to be high, especially when the habitat is well connected (see the fit to the predicted range shift in Fig. 1E, F for low dispersal mortality). In our simulations we only considered competition between species, as we assume this to be the most important interaction for shaping species' niches. Note that in this case the competing species acts as a guarantor of niche conservatism for the first species, an implicit assumption of most BEMs. Even though the first species could in our simulations invade the whole landscape and thus widen its fundamental niche (Fig. 1C, D), it does not, because the habitat is already occupied by the other species, which is better adapted to conditions there. However, as dispersal evolves to low values, local adaptation for both species is necessary to avoid extinction, with the consequence of niches changing. Hence, the assumption of niche conservatism – as it is used by most BEMs – seems to be justified only for conditions that allow high dispersal, in which we conclude that BEMs are adequate, but may be invalid for scenarios with very low dispersal evolving. One has to keep in mind that for reasons of simplicity we modeled symmetric competition with ecologically and evolutionarily equal species. Although more complex interactions are common in nature, we are convinced that the qualitative findings of our study are to a certain degree robust also under these assumptions. One example is given by the study of Jankowski et al. (2010), investigating range shifts of montane tropical bird species. They found that asymmetric interspecific competition leads to stable range borders between species. They conclude that under the assumption of global climate change dominant species with shifting distributions could force subdominant species into smaller ranges. Our results from the two-species scenario show similar patterns, when dispersal mortality is low, without the need for the inclusion of asymmetric competition. Nevertheless we cannot exclude that more complex types of competition (e.g. significantly different degrees of specialization) might still alter range shift predictions even in the presence of high dispersal. More research on the influence of several types of competition, as well as other interactions, like mutualistic, parasitic, or predator–prey systems on BEM predictions is needed. A good example for such research is given by the assessment of the influences of host–parasitoid interactions on the accuracy of BEM predictions that was provided by Zurell et al. (2009).

Future attempts to predict range shifts during global climate change must take care of the landscape configuration in terms of actual connectivity, but also the evolving dispersal potential of species. Of course, incorporating dispersal evolution into BEMs is a challenge that should not be underestimated. In most cases the genetic basis of

dispersal is unknown, as well as potential costs associated with it (Bonte et al. 2012), species have to pay when investing into higher dispersiveness (like decreased fecundity). However, consideration of dispersal evolution may be highly important to improve the predictive potential of bioclimate envelope models. As long as dispersal is likely, the presence of interspecific competition and the possibility for local adaptation might be of minor importance for projecting range changes accurately, simply because dispersal is often the fastest source of beneficial alleles in changing landscapes. However, if habitats are fragmented and/or the dispersal potential of a given species is low and is unlikely to increase during climate change, the accuracy of predictions will decline. In such scenarios species will experience stronger selective pressures for local adaptation, which might save them from extinction.

Acknowledgements – AK was supported by a grant from the German Science Foundation (DFG PO 244/4-1), TH within project CLIMIT (Settele and Kühn 2009) funded by ANR through the FP6 BiodivERsA Eranet.

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