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Issue: *Climate Change and Species Interactions: Ways Forward***Effects of local adaptation and interspecific competition on species' responses to climate change**Greta Bocedi,¹ Katherine E. Atkins,² Jishan Liao,³ Roslyn C. Henry,¹ Justin M.J. Travis,¹ and Jessica J. Hellmann³¹Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, United Kingdom. ²Yale School of Public Health, New Haven, Connecticut. ³Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana

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Local adaptation and species interactions have been shown to affect geographic ranges; therefore, we need models of climate impact that include both factors. To identify possible dynamics of species when including these factors, we ran simulations of two competing species using an individual-based, coupled map–lattice model using a linear climatic gradient that varies across latitude and is warmed over time. Reproductive success is governed by an individual's adaptation to local climate as well as its location relative to global constraints. In exploratory experiments varying the strength of adaptation and competition, competition reduces genetic diversity and slows range change, although the two species can coexist in the absence of climate change and shift in the absence of competitors. We also found that one species can drive the other to extinction, sometimes long after climate change ends. Weak selection on local adaptation and poor dispersal ability also caused surfing of cooler-adapted phenotypes from the expanding margin backwards, causing loss of warmer-adapted phenotypes. Finally, geographic ranges can become disjointed, losing centrally-adapted genotypes. These initial results suggest that the interplay between local adaptation and interspecific competition can significantly influence species' responses to climate change, in a way that demands future research.

Keywords: climate change; competition; geographic range shift; lattice map model; local adaptation; species interactions

Introduction

Much has been penned about the risk of biodiversity loss due to climate change, primarily occurring when species fail to geographically track, or either physiologically or evolutionarily adjust, to climate change.^{1,2} Restrictions on geographic range change could be caused by natural or artificial dispersal barriers, rates of climate change outpacing dispersal capacity, and the appearance of no-analog climates that replace a species' regional niche altogether.³ Restrictions on physiological plasticity and adaptive evolution include limits on stress tolerance and lack of genetic variation.⁴ If populations decline in many locations due to these processes, genotypes or even entire evolutionary lineages can be erased.

With changes in climate come changes in the adaptive landscape. The adaptation landscape is a conceptual framework depicting organismal fitness at a specific geographical location as a function of phenotype. Fitness declines when populations find

themselves moved from the top of a hill (high fitness before climate change) to a hillside or a valley (lower fitness during climate change). If a population possessing sufficient genetic variation can overcome demographic risks, it may be able to climb the hills of a new adaptive landscape. This evolution in response to a changing adaptive landscape has been explored theoretically,^{5–8} and a few recent models have examined how the presence of a population at the top of a fitness peak (local adaptation) affects geographic range shifts and future adaptive evolution under changing climate.^{9–13}

These previous studies suggest that thanks to historic and ongoing local adaptation, climate change can cause a variety of responses, including species that substantially lag behind their climate envelope, elimination of both cooler- and warmer-adapted phenotypes, forced species extinction even when current and future predicted ranges overlap, and splitting of ranges into distinct phenotypes.⁹

Empirical studies also show that climate change may depress population sizes near the edge of a species’ range because of local adaptation.¹⁴ This depression could reduce the potential number of colonists for range expansion until gene flow, an increase in low-frequency alleles, or advantageous mutations enable local evolution.¹⁵

The direct effects of a changing climate, such as changing temperature and precipitation, however, are not the only factors affecting the adaptive landscape of an organism under climate change. Indirect effects, such as interactions among species, can amplify or dampen the fitness effects of climate change.^{16–23} Strong interactions between species can also preclude geographic range change, as higher trophic levels or mutualists cannot colonize new areas if their resources are not already present. Despite previous studies of local adaptation to climate and changing environments,^{24,25} and previous efforts to include biotic interactions in climate change models,^{26–29} few studies have explored the joint effect of local adaptation and species interactions during periods of climate

change (but see Refs. 13 and 29). There are likely to be inherently complicated and potentially chaotic dynamics of interacting species during climate change. Yet, we must explore and understand these dynamics to inform conservation and landscape management.

Local adaptation to abiotic factors within a single species’ range has been demonstrated in many cases, with numerous examples given in Table 1. Local adaptation research is a hallmark of much of plant ecology (e.g., see Refs. 30–36). Fewer studies examine interacting species that are each locally adapted to climatic factors, such that no list similar to Table 1 can be generated for multiple interacting species. One notable exception includes the study by De Block *et al.*³⁷ of the interaction between a damselfly predator and its *Daphnia* prey, as influenced by local climatic adaptation in both species. Finally, interactions themselves can be sensitive to climatic factors. For example, Hillebrand³⁸ demonstrated that elevated temperature reduces richness in benthic microalgal communities through competition, and Barton³⁹ showed that temperature effects

Table 1. Studies showing evidence of local adaptation to climate; listed are those identified by a Web of Science search for “local adaptation” (key words in title) and screened for climatic factors

Kingdom	Order	Family	Genus	Species	Factor	Reference
Animalia	Atheriniformes	Atherinopsidae	<i>Menidia</i>	<i>Menidia menidia</i>	Temperature	93
Animalia	Cladocera	Daphniidae	<i>Daphnia</i>	<i>Daphnia magna</i>	Temperature	94
Animalia	Diptera	Drosophilidae	<i>Drosophila</i>	<i>Drosophila buzzatii</i>	Climate	95
Animalia	Lepidoptera	Lycaenidae	<i>Lycaena</i>	<i>Lycaena hippothoe</i>	Climate	96
Animalia	Lepidoptera	Papilionidae	<i>Papilio</i>	<i>Papilio canadensis</i>	Temperature	97
Animalia	Orthoptera	Acrididae	<i>Melanoplus</i>	<i>Melanoplus sanguinipes</i>	Temperature	98
Animalia	Passeriformes	Sylviidae	<i>Sylvia</i>	<i>Sylvia atricapilla</i>	Precipitation	99
Animalia	Perciformes	Latidae	<i>Lates</i>	<i>Lates calcarifer</i>	Temperature	100
Animalia	Salmoniformes	Salmonidae	<i>Oncorhynchus</i>	<i>Oncorhynchus clarkii lewisi</i>	Temperature	101
Animalia	Salmoniformes	Salmonidae	<i>Salmo</i>	<i>Salmo trutta</i>	Temperature	102
Animalia	Salmoniformes	Salmonidae	<i>Thymallus</i>	<i>Thymallus thymallus</i>	Temperature	103
Plantae	Apiales	Araliaceae	<i>Panax</i>	<i>Panax quinquefolius L.</i>	Temperature	104
Plantae	Asterales	Asteraceae	<i>Carlina</i>	<i>Carlina vulgaris</i>	Climate	105
Plantae	Brassicales	Brassicaceae	<i>Arabidopsis</i>	<i>Arabidopsis lyrata</i> subsp. <i>Petraea</i>	Climate	106
Plantae	Brassicales	Brassicaceae	<i>Boechera</i>	<i>Arabis fecunda</i>	Climate	107
Plantae	Fagales	Betulaceae	<i>Betula</i>	<i>Betula pubescens Ehrh.</i>	Climate	108
Plantae	Fagales	Fagaceae	<i>Quercus</i>	<i>Quercus suber</i>	Climate	109
Plantae	Malpighiales	Salicaceae	<i>Populus</i>	<i>Populus balsamifera L.</i>	Climate	110
Plantae	Pinales	Pinaceae	<i>Picea</i>	<i>Picea sitchensis</i>	Climate	111
Plantae	Poales	Poaceae	<i>Holcus</i>	<i>Holcus lanatus</i>	Climate	35

[This article was corrected on 9 September 2013 after the initial online publication. References 93–111 were added to Table 1 and the reference list.]

on predator activity indirectly affect herbivory by grasshoppers.

These empirical cases suggest that the next generation of climate change models should include both the direct effects of local adaptation and the indirect effects of species interactions. Toward that goal, we explore here how two competitively interacting species may react to climate change using an individual-based model. In this model, one or both species are and can become locally adapted to climate along a shifting climatic gradient. This model allows us to define the adaptive landscape of two species in terms of their climatic tolerance and competitive ability, and enables tracking of the location and fitness of both species during and after a period of climate change.

Methods

Environment and climatic tolerance

To study the joint influence of local adaptation and species interactions under climate change, we ran simulations with an individual-based, coupled map–lattice model. The landscape is a grid of 200 rows (x) by 200 columns (y), with 20% of the cells being suitable as habitat (same for both species) and randomly distributed in the lattice. Each suitable cell (100×100 m) supports multiple individuals of one or both species depending on the species' carrying capacity. The environment is given by a linear climatic gradient (e.g., temperature), θ , that varies across rows (latitude), x . For these simulations, the value of θ is assumed to increase by 0.075°C each row, giving an overall variation of 15°C across the landscape. This gradient is shifted upward steadily over time to reflect climate change. An optimal location (J) is specified where the highest potential population growth rate is obtained and population growth rate declines across rows (x) away from J . In this analysis J is the same for both species and its initial value, 140, is held constant across all simulation experiments.

We modeled two species with potential for local adaptation affecting the probability that an individual at position x will reproduce:

$$\exp\left(-\left(\frac{(\theta(x) - z)^2}{2V_s} + \frac{(J - x)^2}{2W_s}\right)\right), \quad (1)$$

where V_s reflects the extent of individual climatic tolerance (or strength of individual local adaptation) and W_s reflects the range of conditions

that the entire species can tolerate (as in Refs. 5, 9, and 40; Fig. 1). Specifically, V_s determines how steeply an individual's fitness declines as it moves away from its best-adapted condition, and W_s determines how steeply maximum potential reproduction (obtained by an individual optimally adapted to local conditions) declines from J .^{5,9} The model therefore allows for local tuning and climatic niche sorting by genotype (first term) and captures the constraint of a species' evolutionary history (second term).

Local climatic tolerance is captured by a single diploid "gene" in each species.⁹ The mean of the two allele values determines the climatic phenotype z of an individual. An individual with $z = 20$, for example, is optimally adapted in row x where $\theta(x) = 20$. In both species, novel mutations arise in each generation at a rate of 0.001. Mutations can deviate as much as ± 10 , randomly assigned from a uniform distribution. Parents are randomly selected from individuals within a cell and offspring inherit one random copy of the climatic adaptation gene from each parent.

Population dynamics and competition

The two species have discrete generations and reproduce according to an individual-based, stochastic formulation of the multispecies Ricker model:⁴¹

$$n_{\text{off},t+1} = \text{Poisson}\left(\exp\left[r_i\left(1 - \frac{\sum_{j=1}^S \alpha_{ij} N_{j,t}}{K_i}\right)\right]\right). \quad (2)$$

Here, $n_{\text{off},t+1}$ is the number of offspring produced by a single individual (conditional to the probability of reproducing given above) of a given species i ; r_i and K_i are the growth rate and the carrying capacity, respectively, of that species; while $N_{j,t}$ is the number of individuals of species j at time t . The density dependence acts at the cell scale. An interaction matrix (A) describes the influence of one species on another, where the diagonal elements α_{ii} represent intraspecific interactions (here assumed to be equal to 1 for both species), while the off-diagonal elements α_{ij} represent interspecific interactions (i.e., the per capita effect of species j on the growth rate

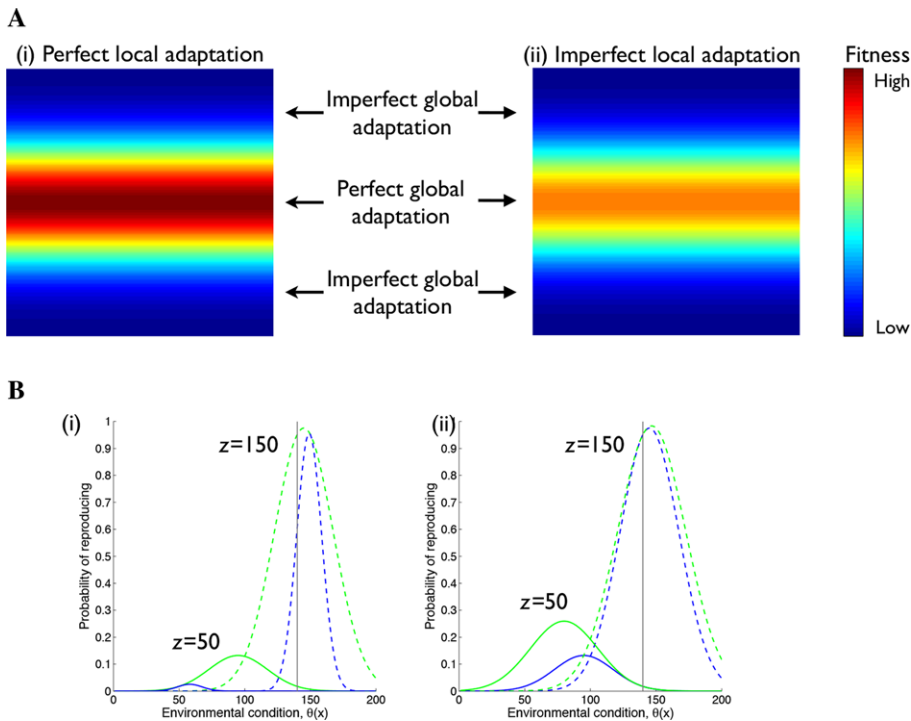


Figure 1. Adaptive landscape for species subject to local and global adaptation along an environmental gradient. (A) Fitness of individuals across a 2D geographic area, where individuals aggregate around the global optimal through the center horizontal line, and are unable to reproduce at the extremes of the environmental gradient (top and bottom where fitness is very low = blue): (1) for a population that is perfectly locally adapted (where the phenotype, z equals the environmental condition, $\theta(x)$), individuals who are perfectly globally adapted (where the individuals' location, x , is equal to the environmental optimum, J) have maximum fitness; (2) for a population that is not perfectly locally adapted, individuals who are perfectly globally adapted remain at a lower fitness. (B) Fitness along an environmental gradient with a global optimal ($J = 140$, gray line) for two phenotypes at $z = 50$ and 150 (solid and dashed lines, respectively). (1) Effect of low (green) and high (blue) selection on local adaptation ($V_s = 1000$ and 100 , respectively) for a given strength of selection for global adaptation ($W_s = 1000$). For low selection on local adaptation, individuals are free to move toward the global optimal, and therefore have a higher overall fitness. (2) Effect of low (green) and high (blue) selection on global adaptation ($W_s = 2000$ and 1000 , respectively) for a given strength of selection for local adaptation ($V_s = 1000$). For low selection on global adaptation, individuals are free to stay near the local optimal and therefore have a higher overall fitness and the species has a wider niche as a whole.

of species i).⁴¹ We assume competitive interspecific interactions, with $\alpha_{12} = \alpha_{21}$ (symmetrical or diffuse competition). Species are not competing for space, as each cell can support both species with independent carrying capacity; however, depending on the strength of competition, species can reduce each other's growth rate.

Dispersal

Offspring disperse from the parent's cell with a certain probability (here constant and equal to 0.2). For dispersing individuals, the distance is drawn from a negative exponential distribution with mean μ (here equal to 400 m for both species), and the direction is randomly drawn from the uniform distribution

($0, 2\pi$). If dispersers arrive in a cell where the habitat is unsuitable, they die.

Simulation experiments

As an initial exploration of the dynamics and possible outcomes for the above model, we performed five simulation experiments (individual runs of the model with contrasting parameter sets). In each experiment, the climate was held stable for 100 generations, shifted from generations 100–200 at a constant speed (v) of one row every two generations (i.e., $v = 0.0375^\circ\text{C/generation}$), and was then held stable again from generations 200–300. This amount of change was chosen because it corresponds to intermediate values in the projection range of recent

global climate models.^{42,43} Simulations started with populations at carrying capacity in all suitable cells for both species. Individuals were initialized to be perfectly adapted to their position along the gradient. In all cases we assumed $r_1 = r_2 = 1.8$ and $K_1 = K_2 = 50$, and we observed the changes in each species' geographic range and the genotypes (locally adapted forms) that persisted through time within that range.

In the first experiment, we considered two species with moderate competition ($\alpha_{12} = \alpha_{21} = 0.5$). Local adaptation occurred in one species ($V_{s1} = 1000$; $W_{s1} = 1000$), while the other had uniform climatic tolerance across the entire lattice (i.e., is a broad-scale climatic generalist). For this scenario we also systemically varied the strength of local adaptation (V_{s1}) and the strength of interaction ($\alpha_{12} = \alpha_{21}$). In the remaining experiments we allowed both species to be locally adapted and focused on fairly strong interaction, with $\alpha_{12} = \alpha_{21} = 0.8$. Specifically, we considered scenarios where the two species had equal climatic tolerance and strength of local adaptation ($V_{s1} = V_{s2} = 1000$; $W_{s1} = W_{s2} = 1000$); differed in the strength of local adaptation ($V_{s1} = 1000$; $V_{s2} = 10^6$; $W_{s1} = W_{s2} = 1000$); differed in the extent of their climatic range ($V_{s1} = V_{s2} = 1000$; $W_{s1} = 1000$; $W_{s2} = 2000$); and, finally, differed in both parameters ($V_{s1} = 1000$; $V_{s2} = 50$; $W_{s1} = 1000$; $W_{s2} = 2000$).

Results

The ability of a locally-adapted species (species 1) to track changing climate was considerably hindered by competition with a second similar species (species 2) that had equal performance over the landscape (Fig. 2). During climate change, species 1 went through a bottleneck and lost its cool-adapted phenotypes when competing with species 2. Increasing the strength of competition exacerbated this effect (Fig. 2C and D) such that when $\alpha_{12} = \alpha_{21} = 0.8$, species 1 was likely to go extinct during the period of climate change (Fig. 2E). These bottlenecks and extinctions occurred despite the fact that both species coexist indefinitely under stable climate, and species 1 was able to track the period of climate change when not competing with species 2 (Fig. 2A and B). After climate change stopped, species 1 was able to evolve again and expand its range to fill the entirety of its new climate envelope. However, this process could take a very long time; for example, with $\alpha_{12} = \alpha_{21} =$

0.65, species 1 had yet to evolve the cooler-adapted phenotypes, and thus expand its range, 100 years after the end of climate change (Fig. 2D).

Systematically varying the strength of selection on local adaptation (V_s) for species 1 and the strength of competition (Fig. 3) showed that interspecific interactions and local adaptation have interacting effects. There are two distinct regions of parameter space where the locally-adapted species either always survived or always went extinct, but there exists a narrow region for both parameters where species persistence was uncertain (Fig. 3A). Interestingly, when extinction occurred in this region, it happened some time after climate change stopped (extinction debt, Fig. 3B). The interaction between local adaptation and interspecific competition determined the initial size of the range, the amount of genetic diversity (Fig. 3C), and the extent of the erosion of genetic diversity during climate change (Fig. 3D).

The combined effects of local adaptation and species interaction produced interesting dynamics in the other experiments. For example, when both species were locally adapted with equal climatic tolerance (W_s) and equal strength of selection on local adaptation (V_s) and under fairly strong competition ($\alpha_{12} = \alpha_{21} = 0.8$), the two species coexisted across their ranges but showed spatial segregation at the range margins under a stable climate (Fig. 4A). During climate change, both species tracked their climatic envelope (Fig. 4B), but the spatial segregation increased, particularly at the expanding margin. Importantly, each species exhibited its fastest rates of spread in those regions where it occurred in isolation from its competitor. By 100 years after the end of climate change, each species had filled up its previous climatic niche, but spatial segregation at the margins remained pronounced.

When the species differed in the degree to which individuals exhibit thermal specialization (different V_s), the initial pattern of species coexistence was similar to the previous example. However, under climate change we observed very different responses. Species 1 (with higher specialization, i.e., lower V_s) was outcompeted by species 2 (with weaker local adaptation, higher V_s) and lost most of its geographic range (Fig. 5). Species 2 retained most of its range but completely lost its warmer-adapted phenotypes and experienced a severe erosion of genetic diversity (Fig. 5). As the

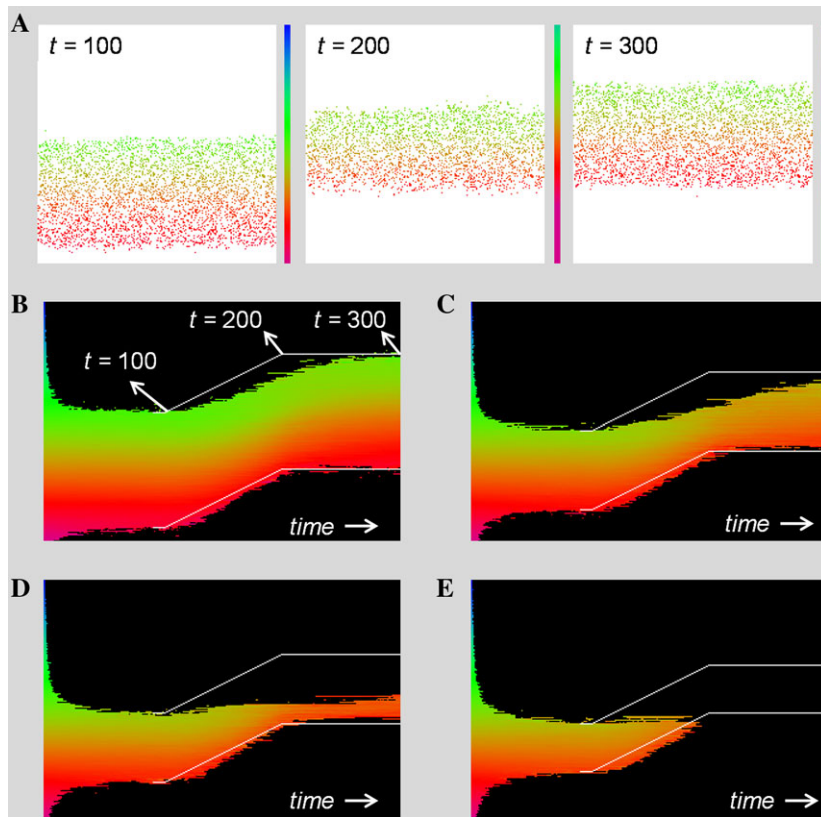


Figure 2. Example of a realization of the model showing local adaptation across the species' range for one locally-adapted species ($V_s = 1000$, $W_s = 1000$). (A) The color bars represent the value of the climatic gradient $\theta(x)$ running from hot (purple) to cool (blue). In each cell, the colors depict the phenotype z averaged across the population (grid cell). The three snapshots from left to right represent the species' range at the beginning of climate change (after 100 years), at the end (after 200 years), and 100 years after climate change ceases (at 300 years). (B) The same model realization is shown, but the spatial grid has been collapsed on the vertical axis and the population's local adaptation and persistence is now followed continuously through time. The white lines represent the climatic envelope for the species: this is drawn based on the relationship between the species' distribution and climate in year 99 and then projected onto future climates. In (C)–(E) we use the space and time approach of (B) to show local adaptation and persistence of the same species as in (A) and (B) when it is competing with a second species that does not show local adaptation (i.e., broad climatic tolerance; all the lattice is equally suitable for it). (C) Moderate strength of competition: $\alpha_{12} = \alpha_{21} = 0.5$. (D)–(E) Increasing strength of competition, (D) $\alpha_{12} = \alpha_{21} = 0.65$ and (E) $\alpha_{12} = \alpha_{21} = 0.8$. Throughout these examples, species 2, which does not have local adaptation, uniformly occupies all the suitable cells, alone or coexisting with species 1 in the regions of overlap. For clarity, the distribution of species 2 is not shown.

climate started to shift, species 2 had a competitive advantage over species 1 because each individual was able to tolerate much broader climatic conditions. Therefore, species 1 only persisted in regions into which it was able to shift. As the two species possess exactly the same dispersal abilities, however, this caused a dramatic reduction in the range of species 1. It only survived in a pocket at the leading edge where, by chance, it was originally the only occupier. Weak selection on local adaptation and relatively poor dispersal ability caused surfing of

the cooler-adapted phenotypes from the expanding margin backwards across the whole range, with consequent loss of the warmer-adapted phenotypes. Even 100 years after climate change, the original genetic diversity had not recovered. However, by varying thermal specialization at the species level (different W_s) so that species differ in the extent of their climatic range but have similar degrees of local adaptation, we found that the species with the broader range (higher W_s , species 2 (Fig. S1)) had no problems shifting its range and retained the whole

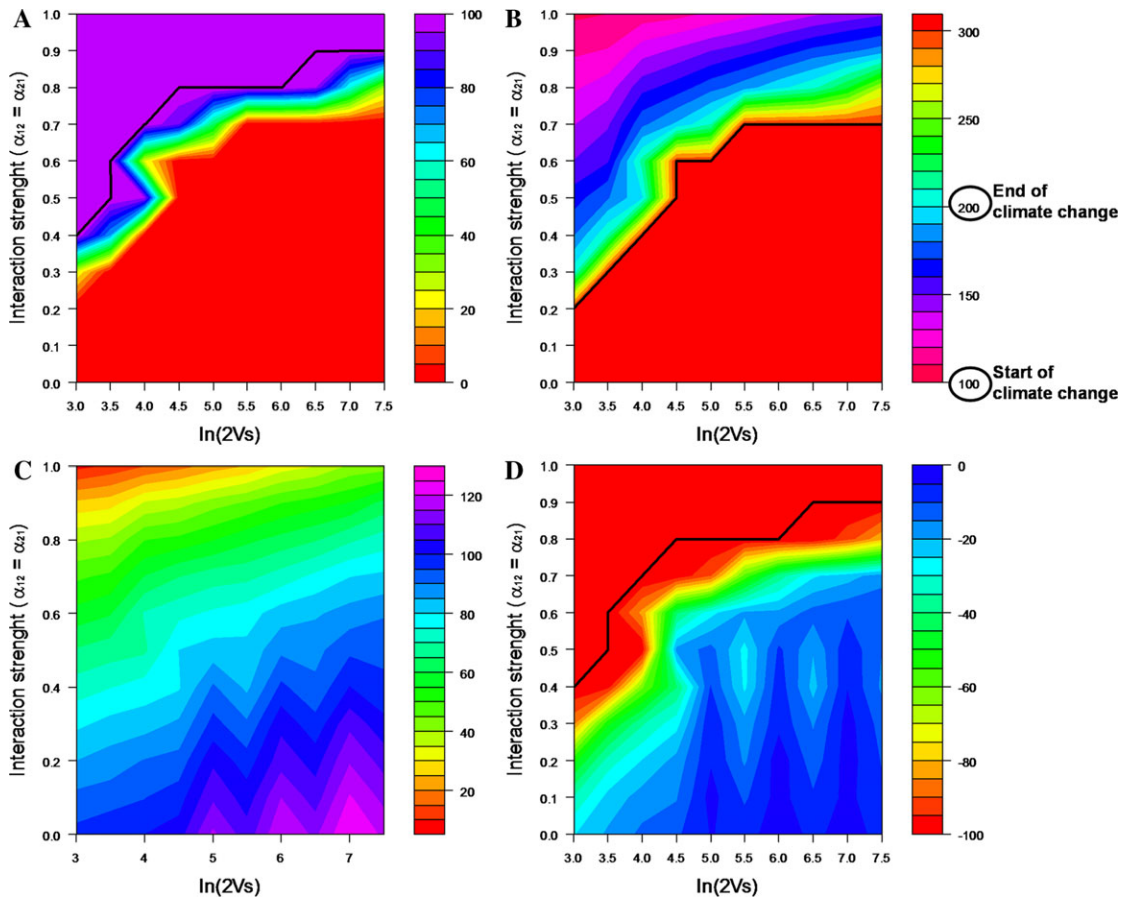


Figure 3. Effect of varying strength of local adaptation (V_{s1}) and strength of interaction with a second nonlocally-adapted species ($\alpha_{12} = \alpha_{21}$) on a single locally-adapted species ($W_{s1} = 1000$). (A) Percentage of extinctions over 20 replicates. The black line indicates 100% extinction. (B) Mean time to extinction. The red area delimited by the black line represents the region of parameter space where extinctions did not occur. (C) Mean range of phenotypes for local adaptation ($z_{\max} - z_{\min}$) just before the start of climate change. (D) Mean percentage reduction of the initial range of phenotypes for local adaptation at the end of the simulation (time = 300). As in (A), the black lines indicate 100% of extinctions (i.e., 100% of phenotypes lost).

range of phenotypes. Conversely, the species with narrower initial range experienced a drastic range reduction, retaining only the phenotypes adapted to its climatic optimum (species 1 (Fig. S1)). This was likely caused by a priority effect, with species 2 occupying the space beyond the expanding margin of species 1, therefore impeding its expansion.

Finally, when species differed in a more complex way, such that species 2 had a broader climatic range (higher W_s) but stronger selection on local adaptation (lower V_s) than species 1, we observed the progressive displacement of species 2 from the area of initial coexistence under climate change (Fig. 6) due to the competitive advantage of the first species. In fact, individuals of the first

species were able to tolerate a broader mismatch between their phenotype and the local temperature, and hence were more resistant to being at nonoptimal conditions, such as during climate change. As a consequence, the range of species 2 became spatially disjointed between its warm and cool portions. The southern populations went almost completely extinct and species 2 lost the core optimum-adapted phenotypes. When climate change stopped, we observed two distinct processes for species 2: the very slow recovery of its remaining southern populations and the gradual expansion southwards of its northern populations with the consequent reappearance of an area of coexistence between the two species. Moreover, the weakened competitive pressure on

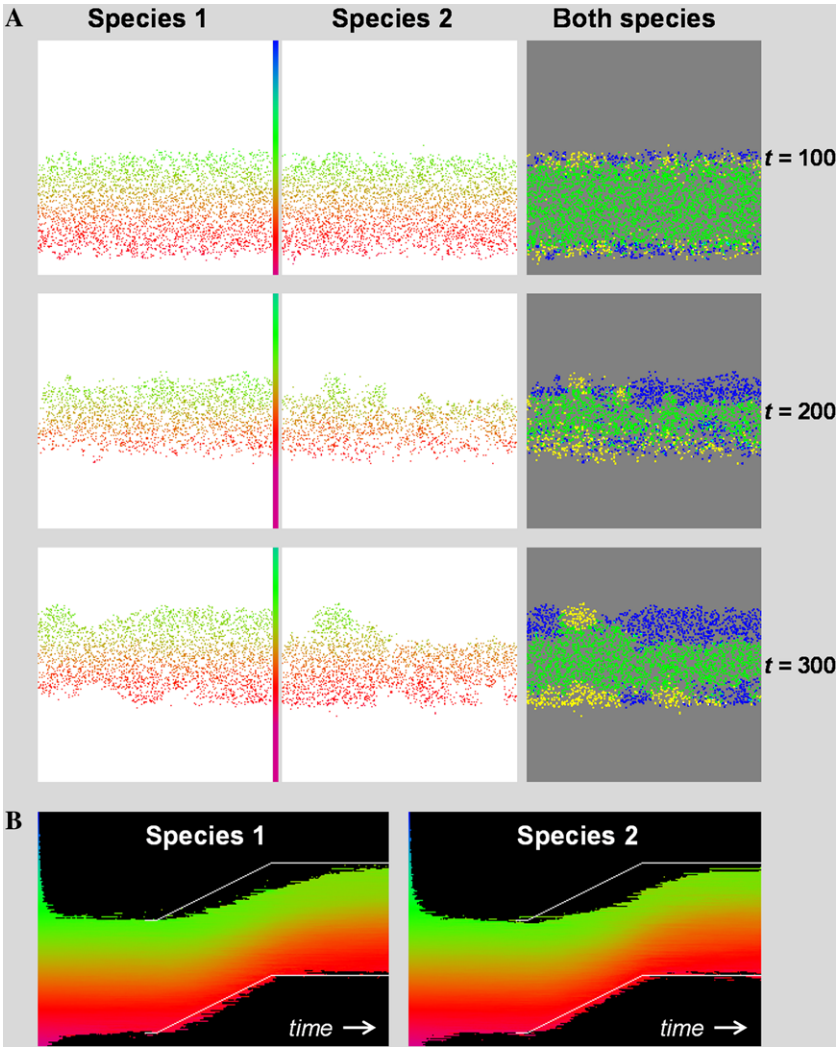


Figure 4. Combined effect of local adaptation and species interactions. The two species are equally locally adapted ($V_{s1} = V_{s2} = 1000$; $W_{s1} = W_{s2} = 1000$) and strongly compete with each other ($\alpha_{12} = \alpha_{21} = 0.8$). (A) Phenotype z averaged across the population (grid cell) at three points in time (after 100, 200, and 300 years) for species 1 (left) and species 2 (center). The right-hand panels represent the species together: blue and yellow indicate the presence of only species 1 or 2 respectively, while green indicates the co-occurrence of both species in the same cell. (B) Phenotype and persistence of species 1 and 2 through time. The color scheme is the same as in Figure 2.

species 1 allowed it to evolve even warmer adapted phenotypes and thereby ending up with a broader range.

Discussion

The purpose of this initial model exploration is to illustrate a variety of ways local adaptation, in combination with species interactions, can mold and modify the responses of species to climatic change. We found a number of nonintuitive outcomes de-

termined by the interplay between the strength of interactions and the strength of selection on local adaptation.

We observed three alternative responses of species to climate change. First, the interacting effect of climate change and a competitor can drive a locally-adapted species to extinction by eliminating its range entirely. Second, a competing species may persist through an episode of climate change by shifting its range, sometimes with a much reduced

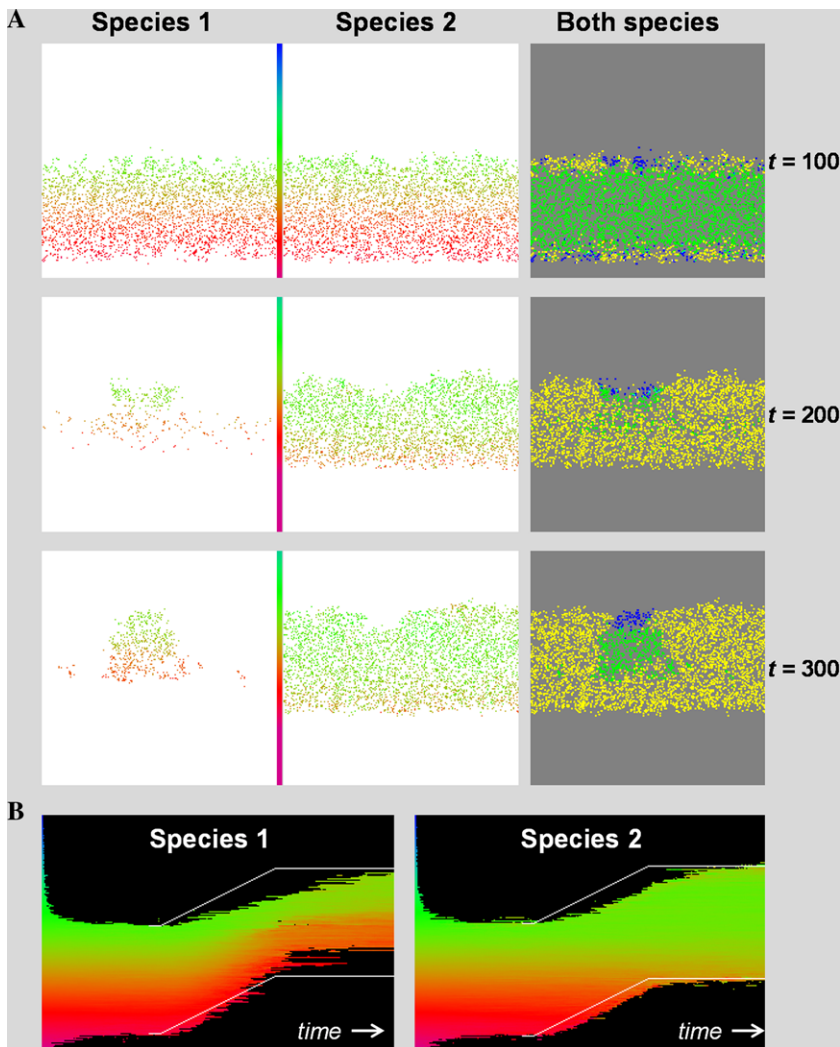


Figure 5. Effect of competition on two species differing in the strength of thermal specialization at the individual level, V_s ($V_{s1} = 1000$; $V_{s2} = 10^6$; $W_{s1} = W_{s2} = 1000$; $\alpha_{12} = \alpha_{21} = 0.8$). (A) Local adaptation phenotype z averaged across the population for the two species (left and center) and species coexistence (right) at three points in time. (B) Phenotype and persistence of species 1 and 2 through time. The color scheme is the same as in Figure 2.

distribution following range shift. Third, a species can persist through climate change and competition but with a substantial reduction of genetic diversity, where a warm or cool genotype begins to dominate the species as a whole.

Competition frequently limited the width of the species' ranges compared to the single-species case,⁴⁴ and importantly, this caused spatial segregation of the two species at their range margins. This is due to competition further reducing the already weak demographic properties of marginal populations, such that once one species is present locally,

a second species has very little chance of becoming established—and, should it do so, its presence will substantially increase the local extinction probability for the first species. Such spatial segregation at the margins may reduce the number of individuals of each species, potentially slowing down range expansion and increasing the risk of local extinction through stochastic events. It is likely to also yield nonobvious and highly stochastic spatial patterns of the species' colonization of the newly climatically available space,^{17,23} analogous to those observed in genetic studies.⁴⁵

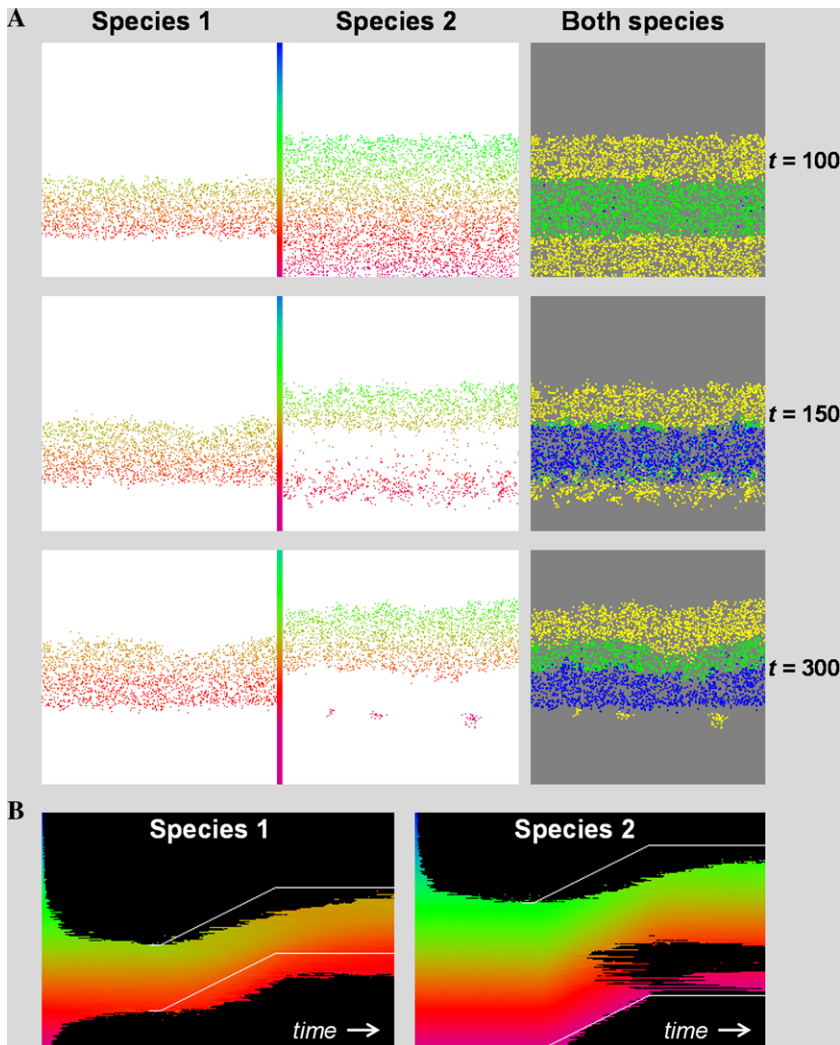


Figure 6. Effect of competition on two species differing in both the strength of thermal specialization at the individual V_s and the species level, W_s ($V_{s1} = 1000$; $V_{s2} = 50$; $W_{s1} = 1000$; $W_{s2} = 2000$; $\alpha_{12} = \alpha_{21} = 0.8$). (A) Local adaptation phenotype z averaged across the population (grid cell) for the two species (left and center) and species coexistence (right) at three points in time. (B) Phenotype and persistence of species 1 and 2 through time. The color scheme is the same as in Figure 2.

Competition hampered the capacity of species to shift their ranges. As the climate starts to shift, species with stronger local adaptation are disadvantaged because of the stronger selection against maladapted phenotypes. Consequently, they are displaced by a more generalist competitor from the regions of previous coexistence.¹¹ This caused a drastic reduction of population size and also sometimes fragmented the species' range.

Our model suggests that the genetic structure of species across their ranges can be substantially modified by climatic change when interspecific

competition and local adaptation are both present. From theory focused on single species, we know that the frontal genotypes leading the expansion process tend to surf backwards across the shifting range,^{45–50} and can ultimately dominate over large spatial extents. However, the addition of interspecific competition and strong, local adaptation substantially complicates this. We found qualitative agreement with this mutation surfing theory only when the species was subjected to a very mild selection on local adaptation and outcompeted the other species early in the climate change phase. In this case

the cold-adapted genotypes at the front essentially surf to high spatial extent and dominate the entire range (Fig. 5). When selection on local adaptation is strong, the surfing backwards of the front genotypes is impeded and, to survive, the core genotypes need to shift their range or evolve again. This, however, can be severely hindered by the presence of a competitor (Fig. 6). It is interesting to consider whether surfing dynamics, shown previously in terms of the genetics of range expansion, might also apply at the species level. When multiple species share a common range margin, then stochastic effects early in a period of environmental change may result in the spreading of a somewhat random set of species, and, in the process, these species may gain an initial advantage that may lead to regional exclusion of other species for substantial periods.

These potentially complex dynamics deserve more thorough investigation, especially since they may have important consequences on the eco-evolutionary dynamics of species facing environmental changes. For example, in our final experiment (Fig. 6), species' thermal niches diverged, not because of divergent selection to climate but because competition determined where a species could persist and, therefore, which climatic genotypes were likely to occur. Moreover, in the case where species have contrasting thermal tolerances, we observed an erosion of central genotypes and the possibility that a species could be spatially segregated, forming two distinct ranges with distinct thermal genotypes. Range split, if also associated with barriers to gene flow, could be a precursor to speciation.^{7,9,51,52}

The effects we observed during the transient phase of changing climate can be long lasting in terms of demographic and evolutionary dynamics. In agreement with Norberg *et al.*,²⁹ for example, we observed extinction debt over a wide range of parameter space. We also saw persistent reductions in population size and genetic diversity. Those species with a high degree of local adaptation are likely to be the most vulnerable, with even very mild competition being sufficient to trigger extinction debt.

Implications

Our results suggest that global-change biologists should consider local adaptation, certainly more than they have in the past, because it can strongly affect the ability of species to track changing climates

geographically and to evolve *in situ*. The potential importance of local adaptation has been argued previously for single species,^{9,14,15} but our results show that local adaptation can strongly affect the responses of interacting species. The vast majority of projection models assume ecological uniformity across species' ranges, and those statistical models that have progressed to incorporate species interactions have typically done so simplistically^{53–60} (but see Ref. 61). If ecological factors like those in our model are representative of nature, we predict that climate envelope models will poorly predict responses. We recognize local adaptation represents an ecological complexity that can be difficult to model, but individual-based approaches such as the one we use here are promising methods for enhancing our understanding of the future biosphere.

Several patterns appear in our results that have direct conservation implications. First, we found spatial segregation of interacting species at shifting range margins, suggesting that species may not widely occur during the shifting process. Second, ecologists often worry about the conservation of cool- or warm-adapted genotypes when the climate changes, but some of simulation results suggest that species could lose the middle portion of their thermal range. Third, in many cases we show that climate change, local adaptation, and competition cause significant reductions in a species' genetic diversity, even when it persists in a large portion of its historic range. Through future mutation and local adaptation, species can regain their genotypic (thermal) diversity, but this recovery process could take thousands of years.

Future research

Future work should systematically explore the three key constraints of this model: strength of interspecific interaction, strength of local selection, and geographic niche (α , V_s , and W_s). It would also be useful to relax the assumptions of competing species having equal demographic parameters and equal dispersal abilities. Species with good dispersal ability, especially those that exhibit fat-tailed dispersal, are expected to have faster range expansions and a greater ability to track climatic shifts.^{62,63} Concomitantly, higher dispersal is expected to be selected for during range expansion, especially at the expanding front.^{64–67} Increased dispersal at an expanding range margin can also have

important genetic effects. On the one hand, it can increase the genetic variance in marginal sink populations, hence enhancing the probability of this population to persist and evolve.^{68,69} On the other hand, high dispersal can increase the maladaptation load in marginal populations, and therefore limit range expansion.^{40,70,71} Norberg *et al.*²⁹ found that, in a multispecies model where locally-adapted species are competing for space, high dispersal increases the probability of species' extinction by increasing species sorting (displacement of marginal maladapted species by preadapted species) at the expense of species persistence. In a model like ours, where species are not competing for space but still can affect each other's reproductive output, asymmetries in dispersal capacities and strength of local adaptation, and the concurrent evolution of dispersal strategies, could potentially change our basic predictions of stronger local adaptation corresponding to higher vulnerability. For example, species with stronger local adaptation could benefit from higher dispersal in a competitive context by forming marginal sink populations that could act as evolutionary stepping stones that could increase the chance of range expansion. Investigating the role of dispersal is particularly crucial, as a recent modeling study somewhat surprisingly concluded that for species with high emigration probability, considering local adaptation and interspecific interactions might be of minor importance for species' responses to climate change.¹³

Further, recent spatial ecological theory has demonstrated that species responding to climate change range shift much less effectively if there is substantial interannual variability in climate.⁷² Thus, one could extend our model to explore how spatial microclimatic variation on top of the environmental gradient influences its dynamics.

Regarding interspecific interactions, it would be important to consider different types of interactions (e.g., asymmetrical and facilitative) using this type of modeling framework.^{17,73,74} The model could also be extended to multiple species ($n > 2$), considering the interplay between different types of interactions and local adaptation, both within and between trophic levels.^{20,21,75–78} Interestingly, in cases where the niche overlap is only partial, interspecific competition could also have the counter-intuitive effect of promoting local adaptation to the changing environment.⁷⁹

Finally, an extension of our model could examine how local adaptation impacts interspecific interactions. For example, the strength and nature of interaction between two species could be temperature dependent or could change along an environmental gradient.^{19,21,37,77,80,81} Moreover, a large body of evidence and theoretical predictions have accumulated on local adaptation and coevolution between interacting species,^{82–90} and how this can be dependent on adaptation to abiotic environment.^{91,92}

The complexity and realism of eco-evolutionary models for climate change could be indefinitely increased, adding more and more components, with the likely outcome of higher complexity. It is therefore crucial to understand the relative importance of the many possible factors and mechanisms that could affect species as the climate changes. Understanding the degree and the parameter space of context dependency in the weight of components such as local adaptation, interspecific interactions, and dispersal will place us in a better position to generalize on species' responses to environmental changes. Most importantly, this will help us develop management strategies that protect biodiversity and ecosystem services as much as possible.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Figure S1. Effect of competition on two species differing in the strength of thermal specialization at the species level, W_s ($V_{s1} = V_{s2} = 1000$; $W_{s1} = 1000$; $W_{s2} = 2000$; $\alpha_{12} = \alpha_{21} = 0.8$). (a) Phenotype z averaged across the population (grid cell) for the two species (left and center) and species coexistence (right) at three points in time. (b) Local adaptation and persistence of species 1 and 2 through time. The color scheme is the same as in Figure 2.

Conflicts of interest

The authors declare no conflicts of interest.

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