Eco-evolutionary responses of biodiversity to climate change

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Climate change is predicted to alter global species diversity[1], the distribution of human pathogens[2] and ecosystem services[3]. Forecasting these changes and designing adequate management of future ecosystem services will require predictive models encompassing the most fundamental biotic responses. However, most present models omit important processes such as evolution and competition[4,5]. Here we develop a spatially explicit eco-evolutionary model of multi-species responses to climate change. We demonstrate that both dispersal and evolution differentially mediate extinction risks and biodiversity alterations through time and across climate gradients. Together, high genetic variance and low dispersal best minimized extinction risks. Surprisingly, high dispersal did not reduce extinctions, because the shifting ranges of some species hastened the decline of others. Evolutionary responses dominated during the later stages of climatic changes and in hot regions. No extinctions occurred without competition, which highlights the importance of including species interactions in global biodiversity models. Most notably, climate change created extinction and evolutionary debts, with changes in species richness and traits occurring long after climate stabilization. Therefore, even if we halt anthropogenic climate change today, transient eco-evolutionary dynamics would ensure centuries of additional alterations in global biodiversity.

Most models of species' responses to climate change explore how dispersal alone affects communities through shifting geographic ranges and ignore species interactions and evolutionary adaptation. However, species interactions often influence responses to climate[6] and climate-related traits can evolve rapidly[7,8]. Adaptation to new climates could moderate the direst predictions of biodiversity loss[9] whereas species interactions could enhance or diminish extinction risks depending on interaction type[10,11]. The available data do not yet permit the incorporation of these processes into quantitative estimates of extinction risk, but given the massive effort required to collect such data, a critical need exists for new theory to identify circumstances under which different processes may be particularly influential. Here we evaluate how ecological and evolutionary processes will interact in mediating species responses to climate change.

To persist despite climate change, species need to disperse rapidly enough to track moving climate conditions, adapt to local conditions, or respond through plasticity[12]. These mechanisms interact with each other and with community dynamics through numerous feedback loops[13,14]. Dispersal can permit range expansion, affect local population size and influence evolutionary dynamics through gene flow[15]. Gene flow between divergent habitats can either swamp or accelerate local adaptation depending on the gene flow-selection balance[16]. Competition can restrict opportunities for adaptation whereas adaptation of resident species can restrict establishment of competitors[14]. Eco-evolutionary dynamics occur frequently in nature[13] and may largely constrain future climate-change responses. However, these eco-evolutionary responses have rarely been explored[14,17].

Here we evaluate how genetic variance and dispersal jointly influence the relative effects of ecological and evolutionary processes on communities along a warming climate gradient. In doing so, we create a more biologically realistic model by allowing ecological and evolutionary processes to interact and for direct and indirect effects of multi-species competition. Both species sorting and local adaptation match species traits to altered local environmental conditions[18,19]. Traits therefore provide a common currency with which to compare ecological and evolutionary responses to climate change. Specifically, changes in the mean community-level trait value (that is, the average trait value across all individuals and species) can be partitioned into that owing to ecological changes in the abundances of species with different traits (species sorting) and to evolutionary changes of traits within species[20] (local adaptation).

We focus here on the temperature optimum for organismal performance as the focal trait and temperature as the key climate variable, but our results apply more generally to any environment-related traits subject to a directionally changing environmental gradient. We assume a continuous parabolic distribution of temperatures (Fig. 1) to create a landscape configuration consistent with a latitudinal temperature change (see Supplementary Fig. S1 for a peaked V-shaped thermal landscape). We then populate the gradient with 21 species, each with a different initial thermal optimum and with genetic variances and dispersal rates drawn randomly from uniform and log–normal distributions, respectively (see Supplementary Methods). Each population has a mean thermal optimum (a quantitative trait) that can evolve in response to selection at a rate proportional to genetic variance. We allow the community to reach ecological and evolutionary equilibrium, then increase global temperature sigmoidally to a maximum at time = 300, at which point climate change ends but simulations continue until time = 1,500 to investigate post-climate change dynamics (Fig. 1).

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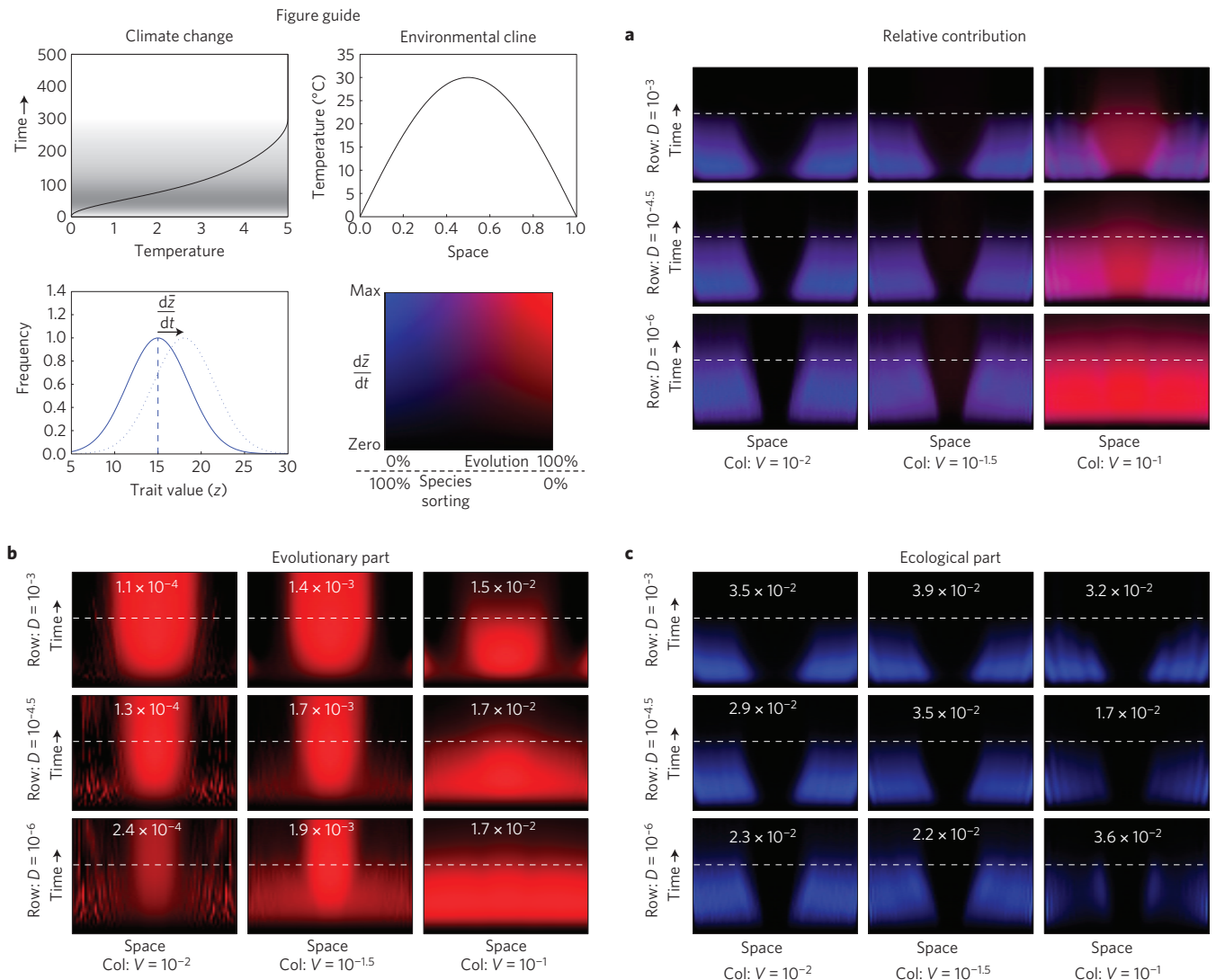
Figure 1 | Relative contribution of evolutionary and ecological processes to change in the mean community trait d$\bar{z}$/dt (guide, lower left panel) over time (y axis, ranging from 0 to 500 generations) and space (x axis) in communities with competition. The local communities occur along a hump-shaped temperature cline over space (guide, upper right panel) and the corresponding change in temperature over time occurs uniformly over this spatial cline (guide, upper left panel). The intensity of blue and red colours indicates the relative proportion of total trait change (guide, lower right panel) for ecological and evolutionary processes respectively (see Supplementary Methods for details of the set-up). **a–c**, Subpanels are arranged with increasing dispersal (D) towards the top and increasing genetic variance (V) towards the right (sigmoid function in time, climate change is zero after time = 300, also indicated as white dotted lines in **a–c**). **b,c**, Highlight the spatiotemporal dynamics of evolutionary and ecological processes by showing the strength of the process relative to the maximum rate (given as numbers in white inside the panels). Note the generally stronger rate of ecological responses but the much longer duration of evolutionary responses.

The relative importance of adaptive evolution versus ecological species sorting (colonization–extinction dynamics that match species' traits to environments) depended jointly on dispersal and genetic variance. With low genetic variance, species sorting played a dominant role in matching community-level trait means to shifting climates (blue region on left subpanels, Fig. 1a). Evolution dominated with high genetic variance and low dispersal (red region on bottom right subpanel, Fig. 1a). Competition narrowed species-range boundaries and decreased the evolutionary responses of cold-adapted species (Fig. 2 and Supplementary Fig. S5; species on edges). Without competition, species respond to climate change mostly through evolution (Fig. 1 and Supplementary Fig. S4) because their fitness did not decline through competition from encroaching warmer-adapted species. This increased fitness provided more time for species to adapt to changing climates before extinction. Results did not

change substantially depending on thermal gradient configuration (Supplementary Figs S1–S3).

Evolution contributed strongly to trait change in new hot climates (Fig. 1b; centre of subpanels) and played a lesser, but important, role in colder environments (Fig. 1b; sides of upper right subpanel). Only evolution allowed species traits to track changing climates in hot regions (Fig. 1) because no species exist to colonize unprecedented hot climates. At mid-latitudes, the arrival of competing species pre-adapted to the warmer conditions hastened the decline of species, thereby thwarting most local adaptation (Fig. 1 and Supplementary Fig. S4). Dynamics were especially interesting in the coldest environments at high dispersal and moderate to high genetic variance. First, the initially high abundances and wide ranges of polar species slowed the expansion of warm-adapted species polewards, thereby delaying species sorting. Second, evolution became more important at the poles
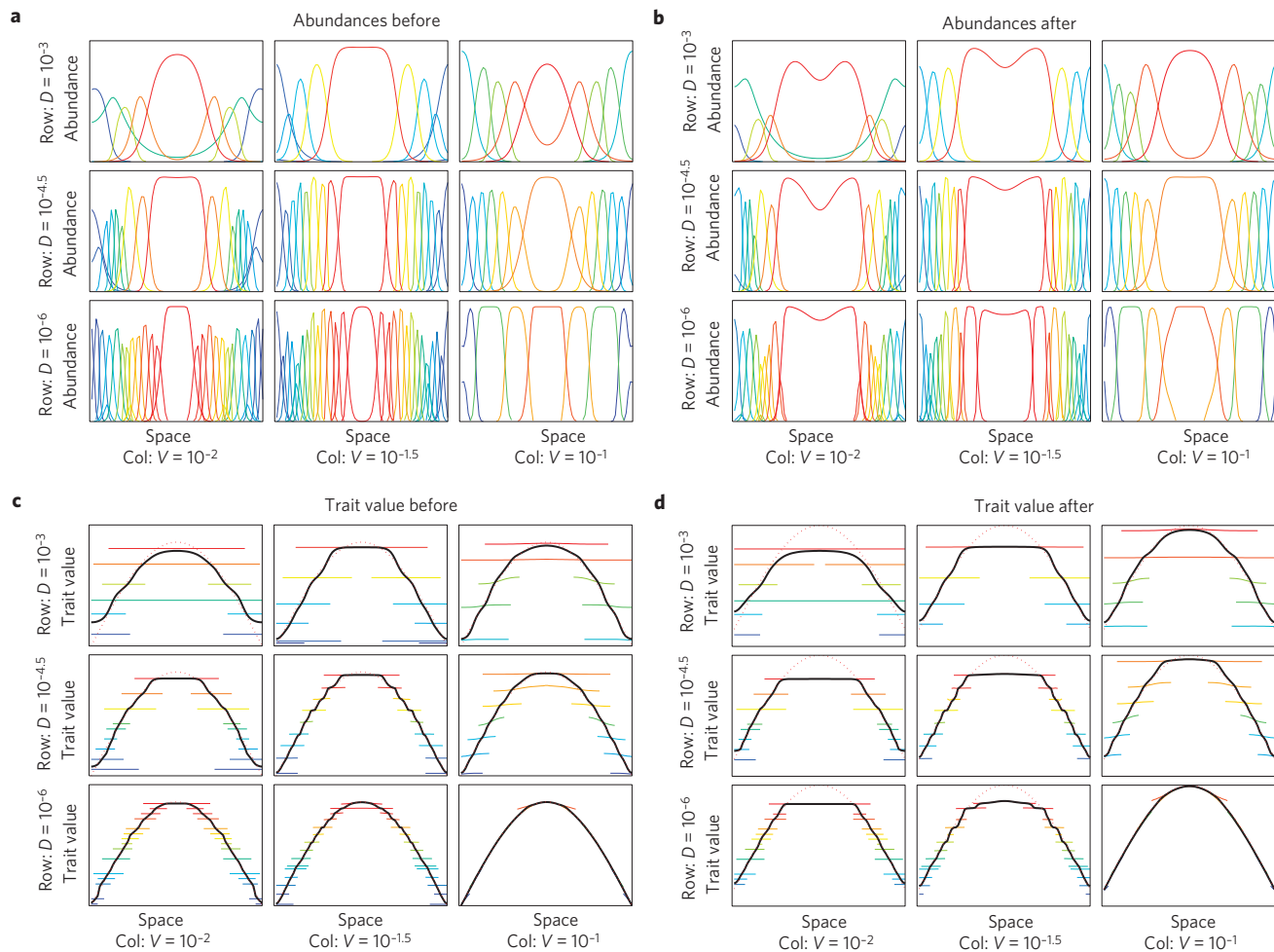
Figure 2 | Species (indicated by different coloured lines) abundances and traits over space (*x* axis for each panel) for different values of *D* (rows) and *V* (columns) before and after climate change has taken place in communities with competition. Abundances before (**a**), abundances after (**b**), trait value before (**c**) and trait value (**d**) after climate change. Black line for trait-value panels shows the weighted community mean and dotted red line shows the optimal trait value determined by the present climate.

than at mid-latitudes because gene flow arrives mostly from warmer places (pre-adapted genes) and not from colder places (maladaptive genes; Fig. 1). Polar species were effectively freed from maladaptive gene flow, but not species sorting, which allowed them to adapt but not to the extent observed for tropical species. To our knowledge this surprising result has not been proposed before.

Most predictions about climate change assume no evolution and no interspecific interactions, with several models suggesting high extinction risks at low dispersal rates[4]. In contrast, climate change caused the most extinctions in our model when dispersal was high and genetic variance low (Fig. 3). Despite the importance of dispersal-fuelled species sorting in the model, evolution was necessary to preserve additional species. High dispersal increased extinctions by making species sorting more effective at the expense of species persistence. This result points out an important shortcoming of climate envelope models that suggest that efficient dispersal will prevent extinction: dispersing competitors can swamp this benefit. We did not explore the evolution of dispersal, but given selection to track changing climates, future models should explore this additional complexity[21,22].

Our results differed from previous predictions because we included competition. Interspecific competition mediated the importance of dispersal and adaptation: all species persisted without competition regardless of dispersal or genetic variance (Supplementary Fig. S6). With interspecific competition, pre-adapted species

displaced even marginally maladapted species. High dispersal did not rescue competing species from climate change for three reasons. First, dispersal actually increased extinction risk by accelerating polar extinctions as warm-adapted species overtook previously cold environments and cold habitats disappeared. Second, high dispersal created asymmetries in species abundances even before climate change, thereby creating rare species that faced increased extinction risk during climate change. Mid-latitude species were squeezed by competitive pressure from expanding tropical species and competitive inertia from slowly declining polar species (Fig. 3). Third, genetic variance was not sufficiently high to rescue species through adaptation.

The model revealed that the ecological and evolutionary processes set in motion during climate change might continue to generate extinctions and trait changes long after climates stabilize. Climates remained stable after time 300, so any subsequent dynamics reflected a delayed response. Most species extinctions occurred after climate stabilization, indicating a substantial extinction debt. Sometimes this extinction debt lasted several hundred years after climate stabilization (Fig. 3, grey shows climate-change rate). In particular, warm-adapted species colonized polar regions, which temporarily increased species richness (blue line in Fig. 3). The warm-adapted species eventually outcompeted the polar species, leading to an overall decline in total species richness. The continuing evolution of species (see evolutionary
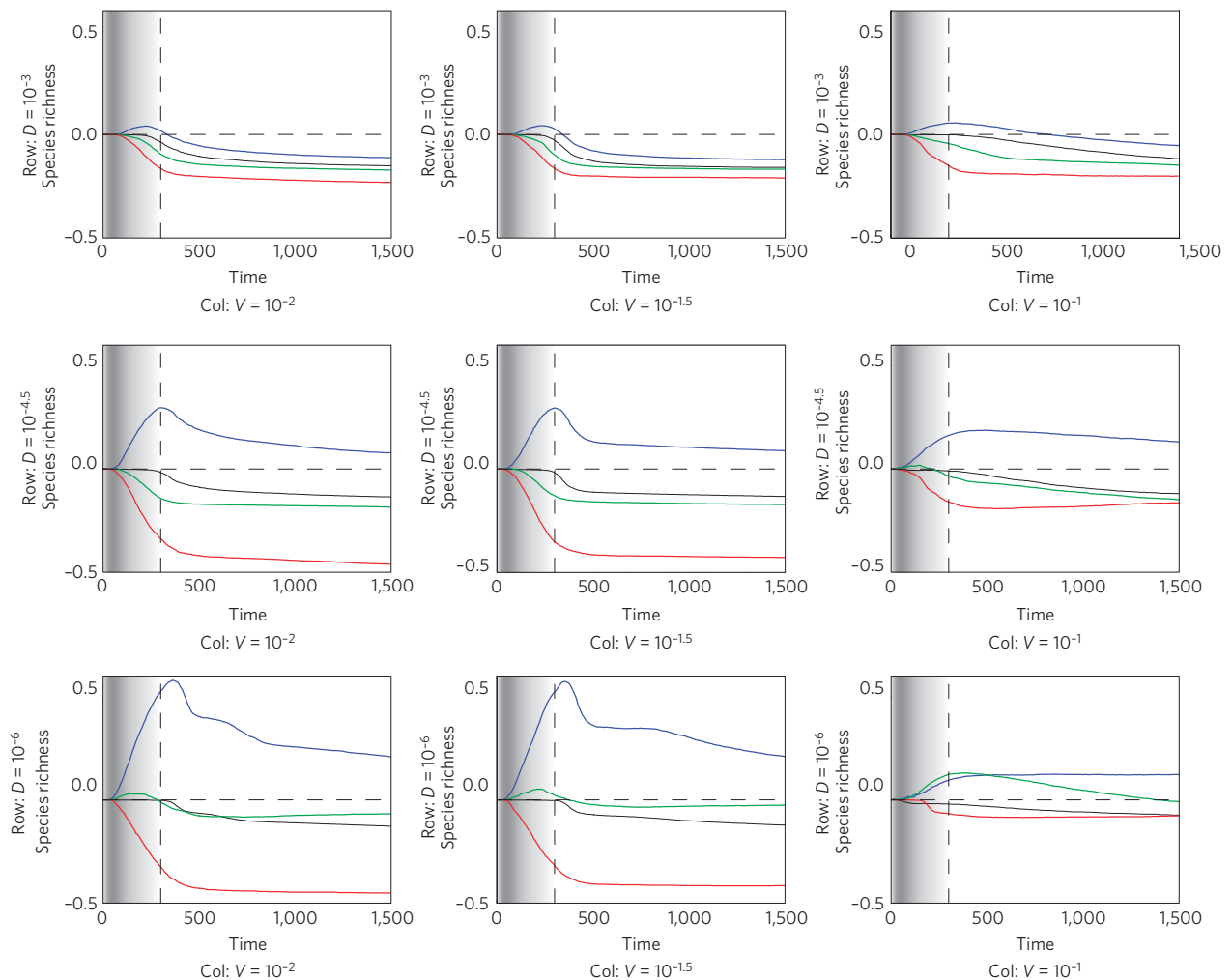
Figure 3 | Time development of the change in species richness during climate change (rate of change in temperature shown as grey shading rate is zero after time = 300 indicated by the dashed vertical line, see also figure guide of Fig. 1, panel for climate change) for the hump-shaped environmental cline. Black gives global richness; blue, green and red shows richness in cold, intermediate and hot regions, respectively.

debt below) and subsequent effects on interactions also probably contributed to extinctions.

An evolutionary debt also occurred, reflecting the protracted time course of adaptive evolution in response to climatic selection (Fig. 1b). The lags observed in tropical areas (Fig. 1b) occurred, in part, because evolution built only on local genetic variance at the trailing edge—no pre-adapted warm genotypes fuelled adaptation to further warming. Because local adaptation was slow relative to gene flow or species sorting (even at higher genetic variances), the evolutionary time lag was substantial, especially at high dispersal rates (top row of Fig. 1b) because of maladaptive gene flow. In contrast, pre-adapted gene flow at the poles created a smaller lag. Lower trait variances in hotter regions supported this interpretation.

Our model emphasizes generality to uncover broad insights. Empirical estimates of key parameters in our model are not yet available for any system. However, median genetic heritabilities range from 0.25 to 0.4 (ref. 23), midway between the intermediate and high values used. Also, empirical studies demonstrate micro-evolutionary responses to climate in many natural populations[24]. At least some species disperse well enough to track present rates of climate change[25] like they do in our model. In an analysis of five past climate-change events in fossil records, a previous study[26] found that adaptation played a dominant role in structuring new communities during the Palaeocene–Eocene Thermal Maximum, as is possible in our simulations under certain conditions (for

example, high genetic variability). More robust empirical tests face the daunting task of measuring or manipulating dispersal, gene flow, genetic variance and competition in many species in numerous places over time. Future empirical progress can be made by focusing on simplified microbial microcosms and field studies. In lab yeast (*Saccharomyces cerevisiae*), persistence during environmental change (salt stress) through evolutionary adaptation depends on the rate of environmental change and the spatial scale of dispersal[27], whereas the presence of pre-adapted types (that is, species sorting) inhibits adaptation to new environments in a lab bacterium (*Pseudomonas fluorescens*; ref. 28). These studies manipulate a subset of factors, but both systems are well suited to manipulating all factors in our model. Field studies can test specific model components. For example, long-term experiments have manipulated both species diversity and key environmental change factors for more than a decade[29], providing an opportunity to test whether species sorting constrains adaptation to environmental change. In the long term, we need more ambitious studies along natural gradients that integrate the key interactions among ecological and evolutionary components of our model.

Tremendous scientific resources have focussed on developing increasingly sophisticated meteorological models of future global climates. In stark contrast, models of future global biodiversity patterns have not yet incorporated the most basic ecological and evolutionary processes. Yet, these processes could alter socio-

economic systems and human health as much as direct climate influences[2,3]. We find that adaptation, dispersal and community dynamics interact in substantial ways. Contrary to conventional wisdom, high dispersal did not preserve all species under climate change because interspecific competition caused extinctions at the poles and for rare species. However, rapid adaptation protected most species when dispersal was low and genetic variance was high, thus placing a premium on the genetic variance necessary to respond to climate change. Although some species have sufficient genetic variance[7], many do not[24], and these species will face extinction as competing species from warmer climates overtake them. Moreover, these threats will not be fully realized until all the extinction and evolutionary debts are paid long after climates stabilize. Future biodiversity changes will spur additional and less predictable impacts on ecosystem services, global food production and human health. Improving biological predictions by incorporating the full suite of interacting biological mechanisms and parameterizing these models for specific ecosystems should be of utmost concern.

References

1. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421,** 37–42 (2003).
2. Gregory, P. J, Johnson, S. N, Newton, A. C. & Ingram, J. S. I Integrating pests and pathogens into the climate change/food security debate. *J. Exp. Bot.* **60,** 2827–2009 (2009).
3. *Millennium Ecosystem Assessment: Ecosystems and Human Well-Being: Synthesis* (Island Press, 2005).
4. Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427,** 145–148 (2004).
5. Urban, M. C., De Meester, L., Vellend, M., Stoks, R. & Vanoverbeke, J. A crucial step toward realism: Responses to climate change from an evolving metacommunity perspective. *Evol. Appl.* **5,** 154–167 (2012).
6. Tylianakis, J. M., Didham, R. K., Bascompte, J. & Wardle, D. A. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11,** 1351–1363 (2008).
7. Franks, S. J., Sim, S. & Weis, A. E. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl Acad. Sci. USA* **104,** 1278–1282 (2007).
8. Balanya, J., Oller, J. M., Huey, R. B., Gilchrist, G. W. & Serra, L. Global genetic change tracks global climate warming in Drosophila subobscura. *Science* **313,** 1773–1775 (2006).
9. Skelly, D. K. *et al.* Evolutionary responses to climate change. *Conserv. Biol.* **21,** 1353–1355 (2007).
10. Brooker, R. W. *et al.* Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *J. Theoret. Biol.* **245,** 59–65 (2007).
11. Münkemüller, T. & Bello, F. de From diversity indices to community assembly processes: A test with simulated data. *Ecography* **34,** 1–13 (2011).
12. Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merila, J. Climate change and evolution: Disentangling environmental and genetic responses. *Mol. Ecol.* **17,** 167–178 (2008).
13. Pelletier, F., Garant, D. & Hendry, A. P. Eco-evolutionary dynamics. *Phil. Trans. R. Soc. Lond. B.* **364,** 1483–1489 (2009).
14. De Mazancourt, C., Johnson, E. & Barraclough, T. G. Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.* **11,** 380–388 (2008).
15. Holt, R. D. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proc. Natl Acad. Sci. USA* **106,** 19659–19665 (2009).
16. Lenormand, G. Gene flow and the limits to natural selection. *Trends Ecol. Evol.* **17,** 183–189 (2002).
17. Case, T. J. & Taper, M. L. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nature* **155,** 583–605 (2000).
18. Ackerly, D. D. Community assembly, niche conservatims, and adaptive evolution in changing environments. *Int. J. Plant Sci.* **164,** S165–S184 (2003).
19. Leibold, M. A., Holt, R. D. & Holyoak, M. in *Metacommunities: Spatial Dynamics and Ecological Communities* (eds Holyoak, M., Leibold, M. A. & Holt, R.) (Univ. Chicago Press, 2005).
20. Collins, S. & Gardner, A. Integrating physiological, ecological and evolutionary change: A Price equation approach. *Ecol. Lett.* **12,** 744–757 (2009).
21. Kubisch, A. *et al.* On the elasticity of range limits during periods of expansion. *Ecology* **91,** 3094–3099 (2010).
22. Burton, O. J. *et al.* Trade-offs and the evolution of life-histories during range expansion. *Ecol. Lett.* **13,** 1210–1220 (2010).
23. Mousseau, T. A. & Roff, D. A. Natural selection and the heritability of fitness components. *Heredity* **59,** 181–197 (1987).
24. Hoffman, A. A. & Sgrò, C. M. Climate change and evolutionary adaptation. *Nature* **470,** 479–485 (2011).
25. Chen, I. *et al.* Rapid range shifts of species associated with high levels of climate warming. *Science* **333,** 1024–1026 (2011).
26. Willis, K. J. & MacDonald, G. M. Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annu. Rev. Ecol. Evol. Syst.* **42,** 267–287 (2011).
27. Bell, G. & Gonzalez, A. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science* **332,** 1327–1330 (2011).
28. Brockhurst, M. A. *et al.* Niche occupation limits adaptive radiation in experimental microcosms. *PLoS ONE* **2,** e193 (2007).
29. Lau, J. A. *et al.* Species interactions in a changing environment: Elevated CO_2 alters the ecological and potential evolutionary consequences of competition. *Evol. Ecol. Res.* **12,** 435–455 (2010).

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Author contributions

All authors conceived the problem and formulated the model. C.A.K. and J.N. coded the model. J.N. ran the simulations. All authors contributed to interpretation of results and writing the paper.

Additional information

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