REVIEW

Climate Change and the Past, Present, and Future of Biotic Interactions

Jessica L. Blois,[1]* Phoebe L. Zarnetske,[2] Matthew C. Fitzpatrick,[3] Seth Finnegan[4]

Biotic interactions drive key ecological and evolutionary processes and mediate ecosystem responses to climate change. The direction, frequency, and intensity of biotic interactions can in turn be altered by climate change. Understanding the complex interplay between climate and biotic interactions is thus essential for fully anticipating how ecosystems will respond to the fast rates of current warming, which are unprecedented since the end of the last glacial period. We highlight episodes of climate change that have disrupted ecosystems and trophic interactions over time scales ranging from years to millennia by changing species' relative abundances and geographic ranges, causing extinctions, and creating transient and novel communities dominated by generalist species and interactions. These patterns emerge repeatedly across disparate temporal and spatial scales, suggesting the possibility of similar underlying processes. Based on these findings, we identify knowledge gaps and fruitful areas for research that will further our understanding of the effects of climate change on ecosystems.

Climate change has occurred repeatedly throughout Earth's history, but the recent rate of warming far exceeds that of any previous warming episode in the past 10,000 years (1, 2) and perhaps far longer. Knowledge of how climate change has altered interactions among organisms in the past may help us understand whether consistent patterns emerge that could inform the future of a warming and increasingly human-dominated planet. The fossil record provides an opportunity to study ecosystems on both ecological and geological time scales but is unevenly distributed across time, environments, and taxa and contains only fragmentary information about biotic interactions (3). Modern systems provide direct, though short-term, observational (4) and experimental (5, 6) evidence of changes in biotic interactions during climate change that together can elucidate important mechanisms driving ecological and evolutionary processes. However, it is not always clear how to extrapolate the insights gained from short-term observations over the longer time scales on which future climate change will play out. Robust predictions about the future require multispecies models that combine long-term insights from the past with more specific and shorter-term insights from modern systems—a herculean challenge, given that models for species responses to climate change have only begun to incorporate biotic interactions (7). Even the term "biotic interactions" means different things to different disciplines. We view biotic interactions in broad terms—namely, as the influence of individuals or populations on one another. In practice, observations from the fossil record and models of the future generally consider the potential interactions of co-occurring species, whereas actual interactions are more easily identified in modern systems. Here we combine insights from past and present-day ecological systems to understand how climate change has affected biotic interactions through time and to identify fruitful avenues for adequately predicting future changes to ecosystems.

How Did Past Climate Change Alter Biotic Interactions?

The geologic record provides unambiguous evidence that some past episodes of climate change have altered biotic interactions by driving extinction and speciation and altering the distributions and abundances of species. The relative diversities of clades and functional groups have varied enormously over geological time [for example, see Fig. 1 for marine genera (8)], and these diversity changes were often accompanied by changes in biotic interactions at both local (9) and global (8, 10) scales. Marine ecosystems, which have the most complete fossil record, exhibit long intervals of relative stability in broad ecological and taxonomic structure, punctuated by short episodes of turnover and ecological upheaval (Fig. 1). These episodes are the well-known mass extinction events (Fig. 1) (11), several of which appear to have resulted from climate change and associated changes such as ocean acidification, eutrophication, and anoxia (12–15).

Mass extinctions illustrate the outcome of complex nonlinear feedbacks between climate change and biotic interactions and offer insights into the types of biotic changes that may be expected in the future. One recurring motif in both marine and terrestrial systems is community homogenization: Mass extinction events are often followed by the establishment, sometimes for hundreds of thousands of years or longer, of assemblages dominated by ecological generalists with broad environmental ranges. The catastrophic Permo-Triassic (PT) extinction (Fig. 1) demonstrates this phenomenon: Rapid warming and ocean acidification probably caused the extinction of a large proportion of marine (12) and terrestrial (16) taxa, and in both realms post-extinction communities were dominated by ecological generalists (17, 18). Similarly, specialized plant-insect associations recovered much more slowly after the end-Cretaceous mass extinction (Fig. 1) and associated climatic changes (19) than did generalist associations (20).

Mass extinction events may continue to affect the structure of biotic interactions long after ecosystems have recovered to pre-extinction diversity levels. In the case of the PT extinction, the ecosystems that arose after the Early Triassic recovery interval show evidence of increased complexity relative to their pre-extinction analogs (16, 21). For example, in the terrestrial realm some vertebrate groups maintained their pre-extinction functional roles, but entirely new functional groups also emerged, in time giving rise to more complex networks of interactions than existed before the extinction (16). In the marine realm, the PT event profoundly altered the long-term diversity trajectories of major taxa (Fig. 1), and relative abundance distributions imply a lasting post-Permian increase in the ecological complexity of benthic communities (21).

Although mass extinctions provide some of the best evidence for altered biotic interactions, networks of biotic interactions (as implied by the composition of fossil assemblages) also change in ways that do not necessarily involve extinction. Climate-mediated dispersal and invasion events are prominent in the fossil record (22, 23) and may provide valuable analogs for the present. A particularly pertinent example is the Paleocene-Eocene Thermal Maximum 55 million years ago (Ma), when a sudden rise in atmospheric greenhouse gases drove rapid global warming (24). In the Bighorn Basin of North America, this event was associated with compositional changes and novel but transitory species assemblages that emerged after range shifts and the immigration of new species (22). In this same region and time frame, rising temperatures led to increased intensity and frequency of insect herbivory on plants (Fig. 2) (25). The link between insect damage and temperature through time is consistent with modern meridional gradients in herbivore damage diversity (26), suggesting that increased insect herbivory may be a persistent effect of future climate warming (25). The Great American Biotic Interchange, facilitated by a combination of tectonic changes from 12 to 3 Ma that formed the isthmus connecting North and South America and climate-driven changes in habitat along the isthmus, offers another example of large-scale faunal interchange (27). During this event, plants

[1]School of Natural Sciences, University of California, Merced, 5200 North Lake Road, Merced, CA 95343, USA. [2]Yale School of Forestry and Environmental Studies, Yale University, 195 Prospect Street, New Haven, CT 06511, USA. [3]Appalachian Lab, University of Maryland Center for Environmental Science, Frostburg, MD 21532, USA. [4]Department of Integrative Biology, University of California, Berkeley, 1005 Valley Life Sciences Building 3140, Berkeley, CA 94720–3140, USA.

*Corresponding author. E-mail: jblois@ucmerced.edu

probably dispersed between North and South America several million years before animals (28), and rates of evolutionary diversification differed within immigrant mammals in North versus South America (27). These differences in dispersal and diversification among taxa suggest that the arrival of new species into each continent greatly modified existing biotic interactions. Transient, novel assemblages were also a common aspect of latest Pleistocene ecosystems (Fig. 2) (9, 29). The formation of novel plant assemblages in eastern North America (29, 30) appears to have been driven by both taxon-specific range and abundance shifts in response to Pleistocene climate change and ecological release after anthropogenically driven megaherbivore extinction (Fig. 2) (9). The persistence of these communities for almost 2000 years (Fig. 2) suggests that novel

assemblages formed by contemporary and future climate changes may be transitory on geological time scales but long-lived on human time scales.

Whereas changes in the distribution and abundance of species suggest underlying changes in biotic interactions, food web reconstructions inferred from functional morphology (31) or stable isotopes (32, 33) offer more concrete evidence. So far, only a handful of studies have directly evaluated changes in food web structure associated with climate change episodes. One such study suggests that the extinction of some large vertebrate groups during the PT events may have altered the structure of terrestrial food webs in ways that made the generalist-dominated post-extinction recovery communities more prone to ecological collapse (34). Stable isotopic approaches are more feasible in younger assemblages with better preservation

and are a promising area for future research. For example, isotope-based food web models indicate that predator-prey interactions changed with deglacial climate change, with some predators switching prey during the Last Glacial Maximum 21,000 years before the present (yr B.P.) and overall increases in specialization by predators (35).

How Does Contemporary Climate Change Alter Biotic Interactions?

Recent observations and experiments show that climatic changes on the scale of years to decades can change the distributions and abundances of species and alter biotic interactions. As in the past, contemporary climate change may lead to novel, altered, or lost interactions through (local) extinctions, range shifts, and changes in relative abundance (36, 37). For example, with rising tem-
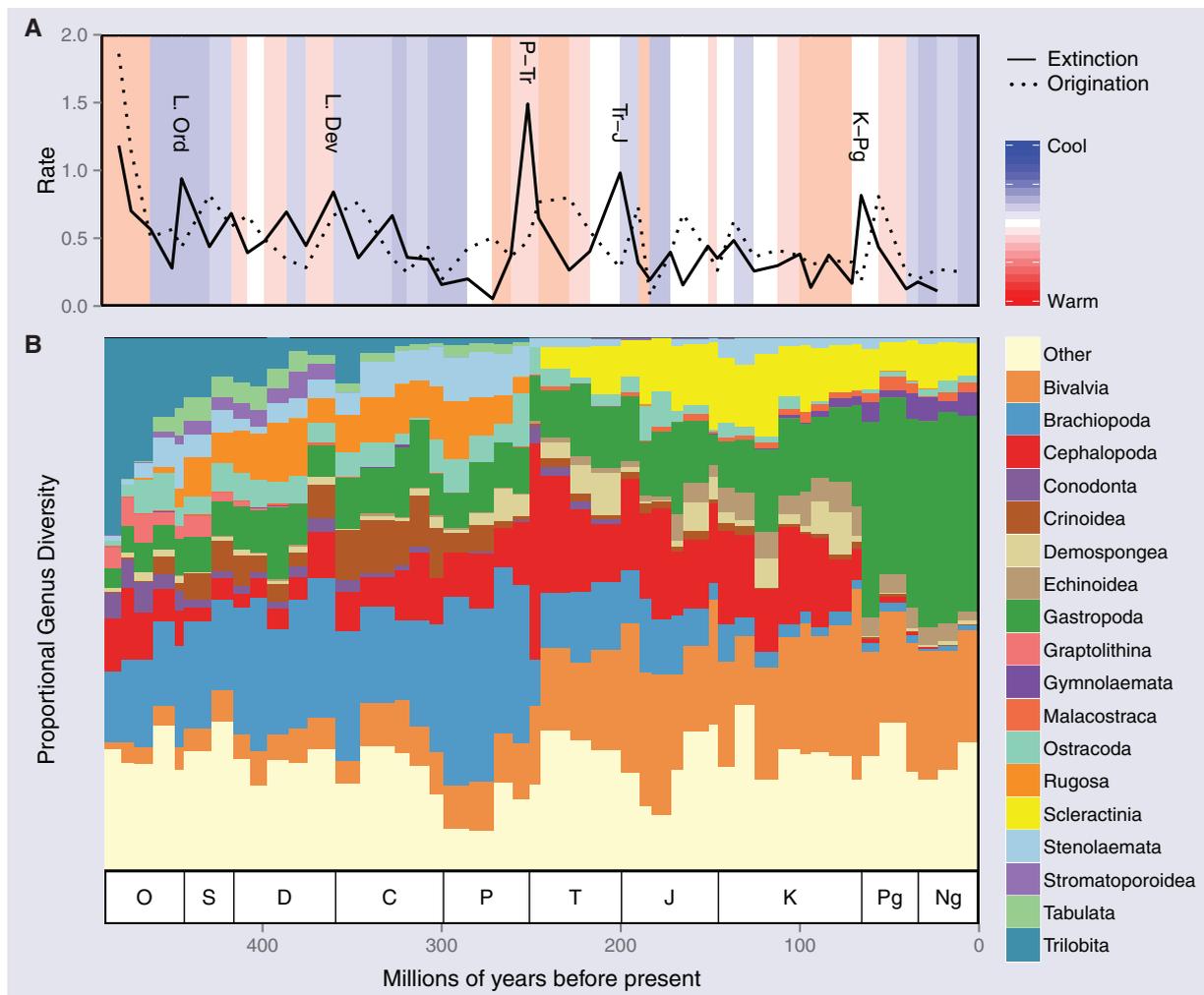

Fig. 1. Macroevolutionary rates and changes in the proportional diversity of fossil marine invertebrate taxa through time and their relationship to broad climate trends. (A) Rates of extinction (solid line) and origination (dotted line) from the Paleobiology Database (8, 85). Colored bands represent relatively warm (red) and cool (blue) intervals and are based on the mean oxygen isotope ratio ($\delta^{18}O$) of well-preserved marine skeletal carbonates (86) after detrending and rescaling to remove the poorly understood long-term Phanerozoic trend toward heavier $\delta^{18}O$ values (86). The "Big Five" mass extinctions are indicated (L. Ord, Late Ordovician; L. Dev, Late Devonian; P-Tr, Permian-Triassic; Tr-J, Triassic-Jurassic; K-Pg, Cretaceous-Paleogene). **(B)** Proportional genus diversity through time, based on genera sampled within each time bin. Age in millions of years before the present and geological periods are indicated along the horizontal axis (O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene).

peratures, species co-occurrence can switch to competitive displacement (*38*), predation can intensify (*39*), or new predator-prey interactions can result (*40*). Fluctuations in climate can also dissipate biotic interactions and allow coexistence by favoring inferior competitors (*36*). In general, climate change should favor species able to tolerate warmer and more variable climatic conditions, resulting in a relative increase in their performance and/or movement to new locations.

Further complexities arise because feedbacks between biotic interactions and climate can lead to larger changes in climate and ecosystem function. For example, changing levels of atmospheric CO_2 may alter the relative abundances of different vegetation functional groups such as woody versus nonwoody plants) and in turn affect ecosystem function even further (*41*). Warming experiments in the Arctic show that higher temperatures favor shrubs (*42*), and these changes in composition can alter regional climate through changes in albedo and evapotranspiration (*43*), a feedback that probably occurred during the mid-Holocene 6000 yr B.P. with expanding boreal forests (*44*).

By 2100, the areal extent of shrubs is expected to expand by 20% (*45*) to 52% (*46*) in areas north of 60° latitude, leading to regional temperature increases via decreased albedo and increased evapotranspiration (*45*, *46*).

Higher trophic levels may be most sensitive to climatic change, and both modern and fossil evidence shows that disrupting their trophic interactions can amplify climate changes throughout the community (*6*, *9*, *47*). At the same time, experiments in aquatic systems show that warming can intensify trophic cascades, leading to stronger control by top consumers, especially keystone species (*39*, *48*). For example, in pitcher plant communities, top-down controls were stronger with warmer temperatures (*49*) and in lower-latitude sites than in higher-latitude sites (*50*). However, climate only accounted for a small amount of the variability in food web structure within these communities along spatial environmental gradients (*51*). Overall, whether warming promotes or weakens trophic interactions, the results are likely to amplify throughout the community (*47*).

Climate-driven changes in phenology (the timing of life history events) are especially likely to alter trophic interactions (*4*), resulting in trophic mismatches (*52*) and community instability (*6*). For example, in parts of the Arctic, caribou mediate the effects of warming temperatures on plant functional groups by reducing shrubs and favoring forb production (*6*). Recent climate change has shifted the peak quality of tundra forage plants to earlier in the year, yet the timing of caribou calving in some regions has not kept pace (*52*), leading to trophic and phenological mismatches. Similar mismatches and/or new associations during climate change can also result from spatial mismatches due to differences in dispersal ability between interacting species (*53*). Vagile species are more likely to track changing climate, whereas dispersal-limited species generally are not (*54*), probably resulting in changes to biotic interactions (*36*, *53*). The superior dispersal ability of a competitor can result in competitive release but also may lead to new competitive matches as novel communities form (*37*). In turn, these novel interactions could result in further changes to community composition because of a lack of coevolved history (*36*) (Fig. 3).

Can We Predict Future Biotic Interactions with Climate Change?

Given the interrelationships between climate change, biotic interactions, dispersal, and community composition, models of individualistic species-climate relationships alone will be insufficient to predict future ecological changes (*53*, *55*). For example, adding occurrences of interacting species (prey availability and predator pressure) improved the performance of correlative species distribution models (SDMs) for the arctic fox (*Alopex lagopus*) in Scandinavia (*56*). Similarly, accounting for dispersal differences and adding a competitor to a SDM helped explain why arctic
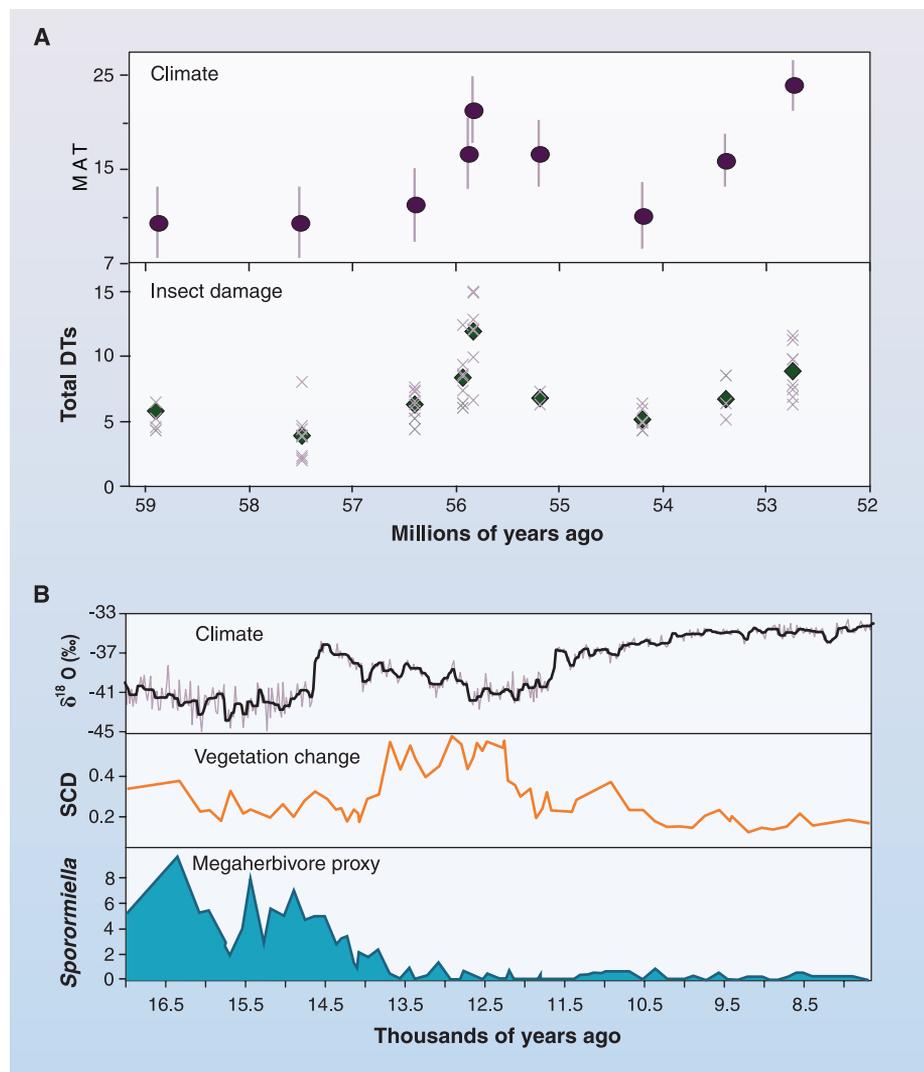

Fig. 2. Biotic interactions through time. (**A**) The top panel shows an index for mean annual temperature (MAT, ±1 SD) based on leaf margin analysis, and the bottom panel shows the number of insect damage types (DTs) across the Paleocene-Eocene Thermal Maximum (PETM). Each X symbol represents the number of DTs on a plant host with at least 20 leaves in the flora; the diamonds are the means of the X's at the site [reprinted with permission from (*25*)]. Insect damage peaked with temperature rise at the PETM. (**B**) Megafaunal extinction and vegetation change across the Pleistocene-Holocene transition (*9*). The black line in the top panel indicates $\delta^{18}O$ from the North Greenland Ice Core Project (*87*). The orange line represents the minimum squared chord dissimilarity (SCD), indicating the dissimilarity of vegetation from that of the present. The blue line represents the abundance of the dung fungus *Sporormiella*, as a percentage of the upland pollen sum, which represents the presence or absence of megafauna. Vegetation dissimilarity peaked after local megafaunal extinction [reprinted with permission from (*9*)].

char (*Salvelinus alpinus*) may not expand into climatically suitable lakes as temperatures warm in the future (*57*).

Despite promising results from SDMs that include biotic as well as climatic predictors, there is a clear need to develop and validate more process-based methods that incorporate multi-species interactions, dispersal, and community assembly to predict communities of the future. Recent work suggests that this might best be realized by examining spatial and temporal patterns of species co-occurrence along environmental gradients (*58*) and by developing dynamic macroecological models that consider patterns of co-occurrence while incorporating (implicitly or explicitly) important ecological processes (*59*). Although a paucity of spatiotemporal co-occurrence data may challenge the parameterization and validation of such models (*55*), the relatively data-rich Quaternary (2.588 Ma to the present) represents an important exception. Pooling data across time may provide more robust estimates of species-climate relationships (*60–62*) and could distinguish species associations that arise because of similar environmental constraints from those due to tightly linked biotic interactions (*63*). Simplifying communities to assemblages of functional groups or traits may also help develop robust predictions that translate across time scales (*64*).

Opportunities for Synthesis

Whereas increased understanding of the ways in which climate change influences biotic interactions is key to making predictions about the future (*36, 65*), substantial challenges remain. A crucial difference between the past and the future is the degree of human alteration of ecosystems. Humans already influence more than 80% of Earth's land surface (*66*), and by 2100, when human population size is expected to double that of today, a quarter or more of the planet could experience climatic conditions that have no modern analog (*67*). The combination of climate change, human land use, and unsustainable harvests may ultimately lead to extinction rates rivaling those of major mass extinctions in the geological past (*68*). Mass extinctions have strongly affected the form and nature of ecosystems throughout time; given the interaction of diverse anthropogenic drivers today and in the future, and especially when considered alongside the ongoing global exchange and spread of invasive species, a future mass extinction event could be accompanied by community reorganization, homogenization, and ecological novelty on an unprecedented scale.

How, then, do we move forward toward a better understanding of the future of biotic interactions? Both the past and present provide important insights regarding the influence of climate change on biotic interactions. We highlight four areas of promising synthesis across time scales that can help anticipate changes in the future: (i)

compile baselines for the relative frequency of specialized versus generalized interactions through time; (ii) elucidate the role of dispersal in mediating changes in biotic interactions; (iii) focus on time-invariant metrics such as interactions between functional groups rather than species; and (iv) use the rich and high-resolution paleoclimatic and ecological data from the Quaternary as a bridge between the ecological time scales of the present and the evolutionary scales of deep time.

Across time scales, we lack baselines for the relative frequency of specialized versus generalized interactions and how that frequency will shift with climate change. For example, a long-held theory in ecology is that specialized interactions should be most prevalent in stable environments, where time and stability allow such tightly coevolved interactions to arise and persist (*69*). In contrast, generalized interactions should dominate regions that have experienced rapid environmental change. Current global biogeographical patterns support these predictions (*70*), and regions where climate fluctuated more strongly during the Quaternary show community structures consistent with a history of disrupted spe-

cies interactions (*71*). Additionally, generalist taxa (*72*) and interactions (*20*) often dominated assemblages after rapid past climate change. When extrapolated to the rapidly changing conditions of the future, tightly coevolved interactions—notably mutualism and parasitism—could be under greatest threat (*36, 73*). Given the projected combination of highly novel environments (*67*) with increasing impacts from other anthropogenic drivers (*74*), rapid biotic turnover, especially where weedy species and pathogens are poised to invade disturbed or weakly coevolved systems, may result in the formation of communities and ecosystems very different from those on Earth today (Fig. 3) (*75*). The combined impacts of extinction and invasion also mean that communities will become increasingly homogeneous in the future (*76*), at least on short evolutionary time scales. However, key issues need to be resolved before we can fully generalize this prediction. First, the definition of what constitutes a "generalist" or "weedy" species or interaction needs to be reconciled across paleo and modern systems. Second, limited evidence from mass extinction events suggests that more-complex ecosystems emerge after the transient rise of generalist taxa,

Fig. 3. Climate change and biological invasions alter the distribution and abundance of species, resulting in novel species combinations and interactions between organisms with no previous history of association. (**A**) Recent increases in minimum winter temperature have allowed the palm *Trachycarpus fortunei* to escape cultivation and invade the deciduous forest of southern Switzerland, far north of other viable palm populations (*88*) [photo credit: M. C. Fitzpatrick]. Novel interactions between species can sometimes cause dramatic and unpredictable changes in ecosystems. By removing the dominant native omnivore, the red land crab (*Gecarcoidea natalis*), and by increasing the populations of two scale insects (*Tachardina aurantiaca* and the nonnative *Coccus celatus*), the invasion of the yellow crazy ant (*Anoplolepis gracilipes*) on Christmas Island altered three trophic levels and led to shifts in the island's rainforest ecosystems from (**B**) an open to (**C**) a dense understory (*89*) [photo credit: P. T. Green]. Symbols are used courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols/).

but whether this pattern holds at other times in the past and whether it emerges on shorter time scales are unknown. Overall, knowledge about the temporal evolution of biotic interaction baselines would itself be highly informative and would also provide the foundation for assessing future changes in biotic interactions.

Another theme that is consistent through time is that novel biotic interactions often arise in rapidly changing environments (*9, 22, 37, 77*) and that dispersal may play a key role in mediating these changes in biotic interactions. Even though contemporary and fossil evidence shows that dispersal differences and biotic interactions can combine to mediate species' responses to climate change (*23, 30, 53, 54*), more research is needed to make explicit links between dispersal and biotic interactions through time. A first step toward this goal would be to examine patterns of species co-occurrence across space and time and determine to what extent the stability of those patterns differs between vagile and dispersal-limited taxa. Related, the geographic distributions of numerous taxa shifted substantially during the late Quaternary, and most studies have attributed these changes to individualistic responses governed primarily by environmental constraints (*78, 79*). However, for range shifts that are not fully explained by climate change, the extent to which the mismatch is due to dispersal limitation versus concerted responses stemming from biotic interactions [or both (*53*)] is unclear (*30, 54*).

The widely disparate observational time scales of the past and the recent present hinder full realization of these emerging insights (*80*), but this problem in part can be ameliorated by controlling for the amount of time across which rates of biotic and climate change are calculated (*68*). Although we lack direct knowledge of the detailed ecology of many extinct species, recent studies have shown that a focus on taxon-free metrics such as functional groups or traits can be informative in making comparisons across time intervals (*34, 64*). An important next step is to extend these efforts to the responses of biotic interactions to climate change across time scales. Similarly, metrics such as community or food web structure that are relatively independent of particular species can provide a "common currency" [(*77*); (*81*), p. 747] and framework for discussing future community and ecosystem changes that translate irrespective of time scales (*82*).

For all of these challenges, further study of the Quaternary record will be of paramount importance. The Quaternary fossil record serves a central role in bridging from the ecological time scales of the present to evolutionary scales seen in deep time. This record is data-rich, and for some systems or sites, time scales of change can be resolved to decades or less (*83*). Climate changes during this period are relatively well understood from independent evidence and models (*84*) and include multiple glacial-interglacial cy-

cles. Quaternary assemblages typically contain many extant species, and genetic and isotopic data are available for many species and assemblages (*35, 78*). Multiple lines of evidence can be used to evaluate the effects of specific climatic drivers on the structure of biotic interaction networks at multiple spatial and temporal scales. Comparisons between modern and Quaternary systems can help illuminate mechanisms and test the generality and permanence of short-term patterns [for example, by teasing apart the roles of climate, CO_2, and fire in functional shifts in vegetation type (*41*)]. Similarly, comparisons between the Quaternary and older intervals can test whether patterns observed on comparatively short time scales hold across longer intervals and elucidate the circumstances under which ecological changes translate into evolutionary change [for example, comparing current and expected future extinction rates to mass extinction events (*10, 68*)]. A detailed examination of the Quaternary fossil record will be key to integrating insights from fossil and extant systems and, ultimately, improving our ability to anticipate the effects of climate change on ecosystems in the future.

References and Notes

1. S. A. Marcott, J. D. Shakun, P. U. Clark, A. C. Mix, *Science* **339**, 1198–1201 (2013).
2. S. Solomon et al., in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, H. L. Miller, Eds. (Cambridge Univ. Press, Cambridge, 2007).
3. A. K. Behrensmeyer, S. Kidwell, R. Gastaldo, *Paleobiology* **26**, 103–147 (2000).
4. L. Matías, A. S. Jump, *For. Ecol. Manage.* **282**, 10–22 (2012).
5. O. L. Petchey, P. T. McPhearson, T. M. Casey, P. J. Morin, *Nature* **402**, 69–72 (1999).
6. E. Post, *Proc. R. Soc.* **280**, 20122722 (2013).
7. M. B. Araújo, A. Rozenfeld, C. Rahbek, P. A. Marquet, *Ecography* **34**, 897–908 (2011).
8. J. Alroy et al., *Science* **321**, 97–100 (2008).
9. J. L. Gill, J. W. Williams, S. T. Jackson, K. B. Lininger, G. S. Robinson, *Science* **326**, 1100–1103 (2009).
10. P. G. Harnik et al., *Trends Ecol. Evol.* **27**, 608–617 (2012).
11. R. K. Bambach, A. H. Knoll, J. J. Sepkoski Jr., *Proc. Natl. Acad. Sci. U.S.A.* **99**, 6854–6859 (2002).
12. J. L. Payne, M. E. Clapham, *Annu. Rev. Earth Planet. Sci.* **40**, 89–111 (2012).
13. S. E. Greene et al., *Earth Sci. Rev.* **113**, 72–93 (2012).
14. T. J. Blackburn et al., *Science* **340**, 941–945 (2013).
15. S. Finnegan, N. A. Heim, S. E. Peters, W. W. Fischer, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 6829–6834 (2012).
16. Z.-Q. Chen, M. J. Benton, *Nat. Geosci.* **5**, 375–383 (2012).
17. J. K. Schubert, D. J. Bottjer, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **116**, 1–39 (1995).
18. S. Sahney, M. J. Benton, *Proc. Biol. Sci.* **275**, 759–765 (2008).
19. P. Schulte et al., *Science* **327**, 1214–1218 (2010).
20. C. C. Labandeira, K. R. Johnson, P. Wilf, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 2061–2066 (2002).
21. P. J. Wagner, M. A. Kosnik, S. Lidgard, *Science* **314**, 1289–1292 (2006).
22. S. L. Wing et al., *Science* **310**, 993–996 (2005).
23. M. O. Woodburne, G. F. Gunnell, R. K. Stucky, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 13399–13403 (2009).
24. J. C. Zachos, G. R. Dickens, R. E. Zeebe, *Nature* **451**, 279–283 (2008).
25. E. D. Currano, C. C. Labandeira, P. Wilf, *Ecol. Monogr.* **80**, 547–567 (2010).
26. J. M. Adams, S. Ahn, N. Ainuddin, M.-L. Lee, *Rev. Palaeobot. Palynol.* **164**, 60–66 (2011).
27. M. O. Woodburne, *J. Mamm. Evol.* **17**, 245–264 (2010).
28. S. Cody, J. E. Richardson, V. Rull, C. Ellis, R. T. Pennington, *Ecography* **33**, 326–332 (2010).
29. J. W. Williams, S. T. Jackson, *Front. Ecol. Environ* **5**, 475–482 (2007).
30. J. L. Blois et al., *Ecography* **36**, 460–473 (2013).
31. J. A. Dunne, R. J. Williams, N. D. Martinez, R. A. Wood, D. H. Erwin, *PLoS Biol.* **6**, e102 (2008).
32. M. K. Schweizer, A. Steele, J. K. Toporski, M. L. Fogel, *Paleobiology* **33**, 590–609 (2007).
33. M. S. Domingo, L. Domingo, C. Badgley, O. Sanisidro, J. Morales, *Proc. Biol. Sci.* **280**, 20122138 (2013).
34. P. D. Roopnarine, K. D. Angielczyk, S. C. Wang, R. Hertog, *Proc. Biol. Sci.* **274**, 2077–2086 (2007).
35. J. D. Yeakel, P. R. Guimarães Jr., H. Bocherens, P. L. Koch, *Proc. Biol. Sci.* **280**, 20130239–20130239 (2013).
36. S. E. Gilman, M. C. Urban, J. Tewksbury, G. W. Gilchrist, R. D. Holt, *Trends Ecol. Evol.* **25**, 325–331 (2010).
37. M. C. Urban, J. J. Tewksbury, K. S. Sheldon, *Proc. R. Soc. B* **279**, 2072–2080 (2012).
38. M. Milazzo, S. Mirto, P. Domenici, M. Gristina, *J. Anim. Ecol.* **82**, 468–477 (2013).
39. C. D. G. Harley, *Science* **334**, 1124–1127 (2011).
40. R. F. Rockwell, L. J. Gormezano, D. N. Koons, *Oikos* **120**, 696–709 (2011).
41. W. J. Bond, G. F. Midgley, *Philos. Trans. R. Soc. London Ser. B* **367**, 601–612 (2012).
42. F. S. Chapin III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, J. A. Laundre, *Ecology* **76**, 694–711 (1995).
43. A. L. Swann, I. Y. Fung, S. Levis, G. B. Bonan, S. C. Doney, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 1295–1300 (2010).
44. J. A. Foley, J. E. Kutzbach, M. T. Coe, S. Levis, *Nature* **371**, 52–54 (1994).
45. C. J. W. Bonfils et al., *Environ. Res. Lett.* **7**, 015503 (2012).
46. R. G. Pearson et al., *Nat. Clim. Change* **3**, 673–677 (2013).
47. P. L. Zarnetske, D. K. Skelly, M. C. Urban, *Science* **336**, 1516–1518 (2012).
48. P. Kratina, H. S. Greig, P. L. Thompson, T. S. A. Carvalho-Pereira, J. B. Shurin, *Ecology* **93**, 1421–1430 (2012).
49. D. Hoekman, *Ecology* **91**, 2819–2825 (2010).
50. D. Hoekman, *Oecologia* **165**, 1073–1082 (2011).
51. B. Baiser, N. J. Gotelli, H. L. Buckley, T. E. Miller, A. M. Ellison, *Glob. Ecol. Biogeogr.* **21**, 579–591 (2012).
52. E. Post, M. C. Forchhammer, *Philos. Trans. R. Soc. London Ser. B* **363**, 2367–2373 (2008).
53. M. C. Urban, P. L. Zarnetske, D. K. Skelly, *Ann. N.Y. Acad. Sci.* 10.1111/nyas.12184 (2013).
54. C. A. Schloss, T. A. Nuñez, J. J. Lawler, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 8606–8611 (2012).
55. M. S. Wisz et al., *Biol. Rev. Camb. Philos. Soc.* **88**, 15–30 (2013).
56. A. R. Hof, R. Jansson, C. Nilsson, *Divers. Distrib.* **18**, 554–562 (2012).
57. C. L. Hein, G. Öhlund, G. Englund, *Ambio* **41**, 303–312 (2012).
58. W. D. Kissling et al., *J. Biogeogr.* **39**, 2163–2178 (2012).
59. K. Mokany, T. D. Harwood, K. J. Williams, S. Ferrier, *Glob. Change Biol.* **18**, 3149–3159 (2012).
60. D. Nogués-Bravo, *Glob. Ecol. Biogeogr.* **18**, 521–531 (2009).
61. S. D. Veloz et al., *Glob. Change Biol.* **18**, 1698–1713 (2012).
62. L. Maiorano et al., *Glob. Ecol. Biogeogr.* **22**, 302–317 (2013).
63. T. C. Giannini, D. S. Chapman, A. M. Saraiva, I. Alves-dos-Santos, J. C. Biesmeijer, *Ecography* **36**, 649–656 (2013).
64. J. T. Eronen et al., *Integr. Zool.* **5**, 88–101 (2010).
65. J. M. Tylianakis, R. K. Didham, J. Bascompte, D. A. Wardle, *Ecol. Lett.* **11**, 1351–1363 (2008).

66. E. W. Sanderson *et al.*, *Bioscience* **52**, 891–904 (2002).
67. J. W. Williams, S. T. Jackson, J. E. Kutzbach, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 5738–5742 (2007).
68. A. D. Barnosky *et al.*, *Nature* **471**, 51–57 (2011).
69. D. W. Schemske, G. G. Mittelbach, H. V. Cornell, J. M. Sobel, K. Roy, *Annu. Rev. Ecol. Evol. Syst.* **40**, 245–269 (2009).
70. M. Dynesius, R. Jansson, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 9115–9120 (2000).
71. B. Dalsgaard *et al.*, *Ecography* 10.1111/j.1600-0587.2013.00201.x (2013).
72. J. L. Blois, J. L. McGuire, E. A. Hadly, *Nature* **465**, 771–774 (2010).
73. R. R. Dunn, N. C. Harris, R. K. Colwell, L. P. Koh, N. S. Sodhi, *Proc. Biol. Sci.* **276**, 3037–3045 (2009).
74. H. M. Pereira *et al.*, *Science* **330**, 1496–1501 (2010).
75. R. J. Hobbs, E. Higgs, J. A. Harris, *Trends Ecol. Evol.* **24**, 599–605 (2009).
76. M. L. McKinney, J. L. Lockwood, *Trends Ecol. Evol.* **14**, 450–453 (1999).
77. M. Lurgi, B. C. López, J. M. Montoya, *Philos. Trans. R. Soc. London Ser. B* **367**, 2913–2922 (2012).
78. E. D. Lorenzen *et al.*, *Nature* **479**, 359–364 (2011).
79. A. Ordonez, J. W. Williams, *Ecol. Lett.* **16**, 773–781 (2013).
80. D. Jablonski, *Evolution* **62**, 715–739 (2008).
81. J. Norberg, M. C. Urban, M. Vellend, C. A. Klausmeier, N. Loeuille, *Nat. Clim. Change* **2**, 747–751 (2012).
82. S. A. Fritz *et al.*, *Trends Ecol. Evol.* 10.1016/j.tree.2013.05.004 (2013).
83. E. C. Grimm, J. J. Donovan, K. J. Brown, *Quat. Sci. Rev.* **30**, 2626–2650 (2011).
84. P. U. Clark *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **109**, E1134–E1142 (2012).
85. 8. J. Alroy, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 11536–11542 (2008).
86. A. Prokoph, G. A. Shields, J. Veizer, *Earth Sci. Rev.* **87**, 113–133 (2008).
87. S. Rasmussen *et al.*, *J. Geophys. Res.* **111**, D06102 (2006).
88. G.-R. Walther *et al.*, *Glob. Ecol. Biogeogr.* **16**, 801–809 (2007).
89. D. J. O'Dowd, P. T. Green, P. S. Lake, *Ecol. Lett.* **6**, 812–817 (2003).

REVIEW

The Future of Species Under Climate Change: Resilience or Decline?

Craig Moritz[1,2,3]* and Rosa Agudo[1]

As climates change across already stressed ecosystems, there is no doubt that species will be affected, but to what extent and which will be most vulnerable remain uncertain. The fossil record suggests that most species persisted through past climate change, whereas forecasts of future impacts predict large-scale range reduction and extinction. Many species have altered range limits and phenotypes through 20th-century climate change, but responses are highly variable. The proximate causes of species decline relative to resilience remain largely obscure; however, recent examples of climate-associated species decline can help guide current management in parallel with ongoing research.

A better understanding of how species respond to ongoing anthropogenic climate change is crucial for assessing vulnerability and guiding efforts to avoid potentially severe biodiversity loss (*1, 2*). However, whereas forecasts of changes in species' geographic ranges typically predict severe declines (*3, 4*), paleoecological studies suggest resilience to past climatic warming (Fig. 1) (*5–7*). Superficially, it seems that either forecasts of future response are overestimating impacts (*8*) or that history is somehow an unreliable guide to the future (*9*). Here, we explore the apparent contradiction between (observed) past and (predicted) future species responses by first summarizing salient concepts and theory, then reviewing (i) broad-scale predictions of future response and (ii) evidence from paleontological and phylogeographic studies of

past responses at millennial or greater time scales. To bridge the two, we consider evidence for responses to more recent (20th-century) climate change. Finally, we place these observations in a management context.

What Theory Says: Concepts and Predictive Models

In principle, the vulnerability of a given species to climate change is a combination of exposure (that is, regional or "mesoscale" change in climatic means and extremes) and intrinsic sensitivity (for example, due to physiological limits, habitat or trophic specialization, life history characteristics, or obligate species interactions). These factors are mediated by response, defined as the capacity of local populations to buffer climatic alterations in situ via plastic reactions (including behavioral responses) or genetic adaptation, or by shifting geographically to track optimal conditions (Fig. 2A) (*1, 2, 10*).

Exposure is typically measured as shifts in mean precipitation or temperature at the mesoscale (e.g., 1 to 100 km²). For temperature, ensemble forecasts tend to predict the largest increases in northern high latitudes and the lowest across

the southern oceans (*11*). Novel climatic conditions, in which new species assemblages might form, are predicted for the tropics, with disappearing climates in the mountains (*12*). The expected increase in frequency of extreme climate events will probably also affect species persistence (*13, 14*). An important consideration here is how landscape features such as slope, aspect, vegetation cover, and soil moisture can ameliorate shifts in means and extremes of temperature at the microenvironmental scale that organisms actually experience (*1, 15–19*). In this context, topographically complex areas provide potential climate change refugia (microrefugia) (*19–22*), whereas low-relief topography can exacerbate climate change impacts, as organisms must move further to remain in the same climate space (*23*). In lowland areas, the requirement to move larger distances to track climate, especially if combined with dispersal limitation due to habitat fragmentation, can cause a lag in the response, possible leading to lowland biotic attrition with important changes in ecosystem functioning (*24*).

A key dimension of species' response is the capacity to persist in situ by altering fitness-related traits by plastic change or genetic adaptation. Plastic responses are undoubtedly important for short-term persistence (*25, 26*), but they can also entail costs (*27*) and may be insufficient to avoid extinction (*28*). Evolutionary rescue requires moderate-to-high heritability of key traits and/or high potential growth rates of populations, with critical levels of these parameters increasing with the rate of change (*29–31*) (Fig. 2B). All of the above is subject to fitness trade-offs across genetically correlated traits, which can further constrain evolutionary response (*32*). So far, and despite abundant evidence for adaptive variation across contemporary climatic gradients, direct evidence of genetically based adaptation to climate change over time remains sparse (*33–36*).

Perhaps the greatest potential for species to respond to climate change rests with local shifts in microhabitat use and dispersal to track suitable

¹Research School of Biology and Centre for Biodiversity Analysis, The Australian National University, Canberra ACT 0200, Australia. ²The Commonwealth Scientific and Industrial Research Organization Ecosystem Sciences Division, GPO Box 1700, Canberra ACT 2601, Australia. ³Museum of Vertebrate Zoology, University of California, Berkeley, CA 94710, USA.

*Corresponding author. E-mail: gekkojessie@gmail.com