



## Predicting the impacts of global change on species, communities and ecosystems: it takes time

What does the future hold for the biological diversity of our planet? Addressing this question is a grand challenge that lies at the heart of many current research programmes in ecology and conservation (Sutherland *et al.*, 2006) and will continue to garner our attention for the foreseeable future. Our understanding of the future is constrained by our limited understanding of the processes that govern how biodiversity originates, is maintained and is diminished. Indeed, the future is rife with uncertainty but this much is clear: human activities are changing the world's climate, reducing and fragmenting habitats and transforming ecological systems globally (Willis & Bhagwat, 2009). There is every expectation that these processes will continue, perhaps at an accelerated pace.

For centuries, biogeographers have noted that the distributions of individual species and species richness both relate strongly to climate (Humboldt, 1855). Many efforts to model species distributions based on present-day climate and forecast future distributions based on future climate scenarios have suggested that extinction rates will rise (Thomas *et al.*, 2004). A key challenge with these approaches is that hypotheses or scenarios foretelling the future can only be directly tested by waiting for the future to unfold, a less than optimal situation for improving our current understanding of forecasting skill. The obvious, albeit incomplete, solution is to use past environmental changes to test whether species, species assemblages and ecosystems have responded in the way that models based on present-day data suggest they should (Araujo *et al.*, 2005).

The need to anchor predictions of the impacts of global change on biodiversity motivated this special issue of *Global Ecology and Biogeography*. Drawing on presentations given to the Ecological Society of America (Pittsburgh, 2010), it is clear that historical perspectives on ecological responses to global change are diverse. Will discoveries about the origins of species diversity illuminate something about how diversity will change in the coming century? What would an ecologist, standing at the warming edge of the last ice age predict for the future of biodiversity, and how would such a prediction stand up against subsequent observations?

Historical studies of this kind have some ingredients in common. Paramount is the availability of ecological observations of the past, whether recent or ancient. Such observations can have many sources, ranging from palaeoecological observations of Mediterranean olive trees to long-term forest monitoring plots on mountaintops. Another ingredient is that each study is strongly quantitative. Historical events can be contingent, even unpredictable, but this does not mean that ecological consequences must also be unpredictable. It is vital to

establish a historical, quantitative baseline of those consequences. They will serve as the foundation for predictions of the future.

Perhaps improving our understanding of the origins of biodiversity will affect predictions of its future. In the contentious area of mechanisms underlying global climate–diversity relationships, there is probably some role for niche conservatism. Rahbek *et al.* (2013) use a global dataset of species richness by latitude to find support for the niche conservatism hypothesis. Their empirical observations support the notion that species richness patterns are largely governed by a clade's ancestral climate affinities. This study takes the term 'historical' to the extreme by using data that spans deep time for the entire globe. Such a deep time view is not merely a theoretical luxury – it may help predict where species persist in times of environmental change, the subject of Levinsky *et al.*'s (2013) paper, which focuses on species persistence in refugia during periods of ancient climate change in Africa. Also focusing on Africa, Huntley *et al.* (2013) use species distribution models to generate a new view about the range of fynbos bird species distributions during the Last Glacial Maximum and to contrast patterns for species range responses during that time between the Northern and Southern hemispheres. The use of a fully coupled atmosphere–ocean circulation model allowed the authors to explore the influence of exposed continental shelf due to sea-level changes on species ranges. Over geological time periods, it might be necessary to account for variation in land surfaces that follow rising and falling sea levels. For those of us whose work focuses on short-lived organisms that rarely appear in fossil records, these views may be particularly striking.

Looking back in time at ecological responses to environmental changes can clearly be very revealing, but what might happen if we stood back in time and looked forward instead? Using the framework that historical observations provide pseudo-experimental tests of ecological models, Williams *et al.* (2013) pose a thoroughly engaging question: what would an ecologist living at the end of the last glacial period propose to conserve species for the impending warming phase? In a clever presentation, they point out that our ancient colleague would probably get the remedy badly wrong and many species would end up moving far beyond the boundaries of the reserves she suggests. Perhaps, over long time periods, this result might seem inevitable, but one of the authors of this work has pointed out similar problems on much shorter time-scales (Kharouba & Kerr, 2010). Williams *et al.* remind us that dynamic environments require dynamic conservation strategies, but that most of those strategies are based on models of a static world.

Palynological data sources have proven particularly effective at illuminating long-term ecological changes. Maiorano *et al.* (2013) use 1000-year time-slice vignettes of the realized niches for three tree species to demonstrate that the realized niche is not static through time. It is mobile within the fundamental niche, and measuring it requires multitemporal analysis. Understanding how species ranges shift through time in response to changing climates requires this kind of insight and might help explain otherwise surprising failures by species to apparently track changing climates geographically. Yet, the palaeoecological point of view provides hope that such predictions may be possible. Macias-Fauria & Willis (2013) use species distribution models to predict changing distributions of tree species in Europe. Fortunately, for species that humans do not cultivate or manage heavily, spatial models of their distributions are transferable in time, an important and useful result.

Static approaches for modelling how diversity changes through time have proved to be challenging. Common statistical techniques, like general linear models, do not account for spatial or temporal autocorrelation in observations and thus can influence model selection and reduce the accuracy of probability tests. Algar *et al.* (2009) showed that predicting change in diversity through time could be accurate, but to minimize biases it was necessary to use regression models that account for spatial autocorrelation. Now, Swanson *et al.* (2013) have provided the first application of generalized linear mixed models that yields improvements to the credibility of predictions of species range changes. Given the imperative to provide transparent estimates of prediction uncertainty, this paper makes a valuable contribution.

Many predictions of how species and ecosystems will respond to climate change make a lot of sense from an intuitive point of view. Dolanc *et al.* (2013) point out one way in which relying on simple predictions in the absence of historical validation can be misleading. A common expectation is that warming in mountainous areas should push subalpine coniferous ecosystems off the tops of mountains. Broadleaf-dominated forests at lower elevations should be creeping higher on these mountains, slowly strangling the mountaintop forests. Using long-term forest plot data, Dolanc *et al.* show that increased warming and precipitation is facilitating the survival of young trees, contributing to the mortality of old trees but leaving modern species composition statistically indistinguishable from historical composition. These high-elevation forests do not yet appear to be going anywhere, despite the onset of a warmer and wetter climate. Intuitive expectations that biotic communities on mountaintops might be pushed into oblivion may simply be wrong. Have predictions of the impacts of climate change on extinction rates been overstated in such cases?

It is clear that predictions of the future are clouded by many uncertainties and that validation of those predictions needs to be far stronger than has yet been commonly possible. In many regions where the impacts of climate change on geographical ranges were first documented, range shifts in recent decades appeared to track changing temperatures. Such observations matched expectations, yet many inconsistencies are known, with some species moving in directions opposite to expectations based

on observed temperature change. Smith has explored the climate spaces where mammal species ranges in mountainous western North America have moved in recent decades, again using a powerful historical model projection framework (Kerr *et al.*, 2007). As other macroecologists have noted (e.g. Hawkins *et al.*, 2003), the interaction between temperature and precipitation is also a significant factor limiting geographical ranges. Measuring how this interaction has changed over the century time-scale of this study is necessary to understand range dynamics through time. It is possible for an area to become unsuitable for a species because of the onset of a kind of forbidden environmental combination, even though neither temperature nor precipitation regimes, respectively, exceed these species tolerances. Addressing the potential impacts of interacting climatic changes on recent and future species distributions is both urgent and difficult.

Lessons from historical analyses of the biotic impacts of climate change are emerging with greater clarity. Predictions of how the geographical ranges of individual species may shift as climates change have the potential to be accurate, but there are too many surprises along the way to accept those predictions uncritically or without rigorous, temporal validation. The tools for building these predictions are getting stronger and their thoughtful use will improve these efforts. Understanding of the origins of biological diversity is likely to be useful in predicting its eventual fate. It is clear that the use of these historical perspectives on how species, biotic communities and ecosystems have responded to past environmental change yields many surprises and insights that are relevant for understanding the biotic consequences of expected global change. Which of these insights will be most critical for reducing global change-induced extinctions in the future? Only time will tell.

Jeremy T. Kerr<sup>1\*</sup> and Solomon Z. Dobrowski<sup>2</sup>

<sup>1</sup>*Department of Biology, University of Ottawa, Ottawa, ON, Canada K1N6N5,*

<sup>2</sup>*Department of Forest Management, University of Montana, Missoula, MT59812, USA  
\*E-mail: jkerr@uottawa.ca*

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