

June 2015

In partnership with the Centre for Biodiversity and Environment Research at University College London



# Climate change and challenges for conservation

DR MARIA DICKINSON, PROFESSOR IAIN COLIN PRENTICE AND PROFESSOR GEORGINA M. MACE

## The headlines

- Biodiversity has been significantly depleted by non-climatic factors, such as land-use change. Climate change will exacerbate this loss and compromise ecosystem integrity.
- Integrated approaches will be necessary to evaluate species' responses to climate change, which will be more complex and more uncertain than range shifts alone.
- This paper recommends applying new perspectives to traditional conservation practices. A global and flexible approach to biodiversity protection and resource management may be needed for successful conservation policy and planning.

## Executive summary

CHANGES IN BIODIVERSITY SINCE THE 1950s DUE TO HUMAN ACTIVITIES HAVE been more rapid than at any time in human history<sup>1</sup> and according to some, we are currently living “amid a global wave of anthropogenically driven biodiversity loss”<sup>2</sup>. To date, much of this loss has been driven by pressures such as population and economic growth and land-use change<sup>3</sup>. These pressures are anticipated to intensify as a growing human population puts increasing pressure on Earth's biological systems and finite resources<sup>4-6</sup>.

Climate change is predicted to have major implications for species and ecosystems, acting as a driver of biodiversity loss in its own right and amplifying the effects of existing threats<sup>7-9</sup>. It differs from other threats, such as land-use change or over-exploitation, in the global extent and pervasive nature of its potential impacts on biodiversity<sup>7,10-12</sup>. This briefing paper asks, to what extent does climate change require a re-think of conservation policy, planning and practice?

Species are predicted to shift their geographic ranges, relative abundances and seasonal timings in response to changing temperature and rainfall patterns<sup>7,10</sup>. Changes in community composition are anticipated to result as spatial or temporal associations between species are disrupted, leading to breakdown of inter-species interactions<sup>7,13</sup>. Where natural or human barriers prevent species from shifting their geographic ranges to track suitable climate, extinction is predicted to result<sup>7,14,15</sup>.

## Contents

Executive summary .....	1
Introduction .....	2
Current and past responses to climate change .....	4
Lessons for conservation in a climate change context .....	7
Conclusions and recommendations ..	15
Acknowledgments.....	15

Grantham Briefing Papers analyse climate change and environmental research linked to work at Imperial, setting it in the context of national and international policy and the future research agenda. This paper and other Grantham publications are available from [www.imperial.ac.uk/grantham/publications](http://www.imperial.ac.uk/grantham/publications)

Land-use change is predicted to be most intense in the biologically rich tropical regions, as economies develop<sup>5,16</sup>. Concentration of small-range, endemic species, which are likely to have narrow climatic tolerances, may also make these regions among those most vulnerable to climate change<sup>17–21</sup>. Tropical regions may, therefore, become centres of biodiversity loss<sup>16,18</sup>. Current bias of financing and expertise, as well as data and understanding of species and ecosystems towards high latitude temperate nations presents a global challenge for conservation<sup>22</sup>.

The potential magnitude of climate change impacts calls for a policy response, but the type of response and the species or regions to be targeted remain unclear. Predictions for wide-scale extinction and disruption of communities and ecosystems have led some to question whether traditional conservation practices, such as protected areas, will continue to be effective<sup>23</sup>. Others have called for radical and interventionist strategies, such as moving species from their current locations to regions that are predicted to be climatically suitable<sup>24,25</sup>.

Alarming, and controversial, predictions for future levels of extinction risk have been widely publicised and have influenced conservation policy and planning<sup>15,26–29</sup>. Such predictions are based on species' abilities, or lack of ability, to shift their geographic ranges in order to track changing climate. Evidence from past and present episodes of climate change suggests that these predictions are not capturing the full range of possible responses<sup>30</sup>. Range shifts alone do not provide an accurate estimate of global extinction risk and may give a false sense of the certainty and predictability of climate change impacts on biodiversity<sup>7</sup>.

The emerging science of integrated vulnerability assessment uses multiple sources of information, such as species' responses to past and present episodes of climate change, along with modelling, theoretical and experimental approaches to better understand and predict the impacts of climate change on biodiversity<sup>30</sup>. Predictions are based on greater understanding of the mechanisms and drivers of vulnerability, so are better able to inform conservation decision-making<sup>30</sup>. Identification of proxies and predictors for sensitivity and adaptive capacity, such as biological traits and taxonomic or regional patterns in vulnerability, as well as understanding of the potential limitations to species' responses, is needed to increase predictive ability<sup>19,21,30</sup>.

Conservation practice does not, in the authors' view, need a complete re-think to accommodate climate change. Application of orthodox conservation actions, such as habitat restoration or the establishment and maintenance of protected areas, will remain the key pieces in a conservationist's tool belt<sup>31–33</sup>. Instead, a new attitude may be more commonly required. Conservation has traditionally aimed to preserve current species and communities in particular habitats. Climate change may make this an impossible task.

Management will need to embrace change, shifting its perspective from preserving current ecosystems to managing and supporting the dynamic responses of species and ecosystems to climate change<sup>33,33</sup>. Where species are shifting ranges or changing their interactions, focus may need to be more on ecological role within a target ecosystem than on species identity<sup>34</sup>. Where climate change is driving transition towards a new ecological state, focus may need to be on facilitating that transition, minimising species loss and preserving key ecosystem functions and services, where possible<sup>33,34</sup>.

Uncertainty in predictions means that a flexible approach is required for conservation planning<sup>35</sup>. Adaptive management, in which management actions are continually monitored, evaluated and modified in response to observed changes, and scenario planning approaches, in which uncertainty is explicitly incorporated by setting goals for a range of futures, should be applied to improve the effectiveness of conservation decision making and implementation of interventions<sup>30–33</sup>.

## Introduction

Climate influences how species live and reproduce<sup>36–39</sup>, their geographic distributions<sup>40</sup> and the structure of the habitats, communities and ecosystems of which they form part. It determines the locations and extents of ecosystems, such as savannahs, deserts and tropical forests, shapes species' ecology, physiology and anatomy, as well as variation in gene frequencies<sup>10,41,42</sup>. This variation in biological systems, termed "biodiversity" (see Box 1), is the foundation of a biologically functioning world. It is necessary for the continuation of ecosystem services on which human health and wellbeing rely, such as cycling of water, carbon and nitrogen, the provision of food, timber, fibre and cotton, and regulation of pests and diseases<sup>3,6</sup>.

Biodiversity is already being severely depleted by non-climatic factors<sup>3</sup>. Conversion of land to human uses, such as agriculture and the building of roads, dams and cities, has degraded, fragmented and eliminated natural habitats, driving species declines towards extinction and reducing the ability of species to move across the landscape<sup>2,3,7</sup>. Extraction of timber, meat, fish and other products has led to substantial declines and, in some cases, collapses of target populations<sup>43,44</sup>. Approximately 40% of invertebrate species that have been assessed are estimated to be threatened or endangered. Populations of terrestrial vertebrate species have declined by an average of 28% during the last 40 years, with associated declines in ecosystem services<sup>2</sup>.

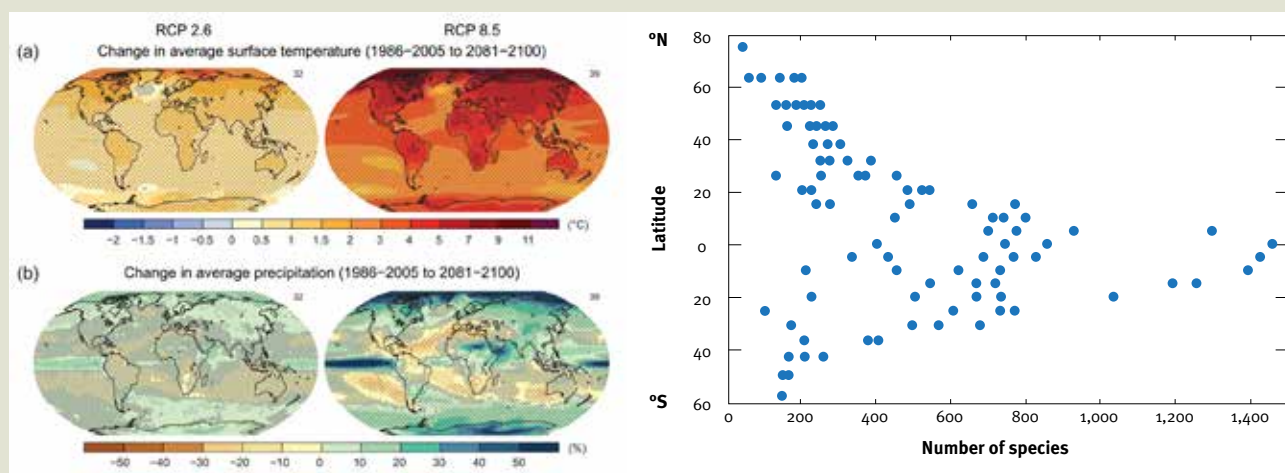
For each of the last three decades, surface temperatures have been successively warmer than any decade since pre-industrial times and global average temperature has risen by 0.85°C since 1880<sup>45</sup>. Climate change for the 21<sup>st</sup> century is projected to be large and rapid. Based on current emissions trends, an average increase in the mean surface temperature of 4°C by

### Box 1: Biodiversity and climate change

Biodiversity is more than just species diversity. It is the sum of all organisms on Earth, their relative abundances, their genetic and phenotypic variation and the communities, ecosystems and biomes of which they form part<sup>6,47</sup>. Biodiversity loss is more than simply species extinction. It is any loss of biological diversity, including local or global loss of genes, phenotypes (anatomy, physiology or behaviour) or species. Biodiversity change includes change in the frequency of genes or abundance of phenotypes or species, but also changes to species' geographic distributions, interactions and communities<sup>6</sup>. Change to or loss of biodiversity may lead to decreases in the functional efficiency, stability or productivity of ecosystems, with consequent effects on ecosystem goods and services<sup>47</sup>.

Climate change is not projected to be uniformly distributed. The magnitude of climate change and whether that change is principally to temperature, rainfall or both is projected to vary geographically. Temperature changes are generally projected to be greatest in high latitude regions, such as the Arctic and Antarctic. At tropical latitudes, the absolute magnitude of warming may be less but rainfall is predicted to be the main axis of change.

Biodiversity is not uniformly distributed. Species numbers follow a latitudinal gradient, with species being concentrated in tropical latitudes<sup>42,152</sup>. Tropical latitudes also contain a larger number of small range and endemic species (species unique to a particular geographic region)<sup>20</sup> (Box 1 Figure 1). For example, "biodiversity hotspots", represent just 2.3% of land surface, but contain more than half of the world's endemic plant species and nearly 43% of bird, mammal, reptile and amphibian endemic species<sup>153</sup>. The majority of these biodiversity hotspots are concentrated in the tropics. Biodiversity loss due to climate change will depend on the complex interplay between geographical patterns in biodiversity, the nature and magnitude of climate change and the effect of other human pressures, such as land-use change<sup>16</sup>.



**Figure 1:** Geographical patterns in climate change and species richness. **Left panel:** Maps of CMIP5 multi-model mean results for the scenarios RCP2.6 and RCP8.5 in 2081–2100 of (a) annual mean surface temperature change, (b) average percent change in annual mean precipitation. The number of CMIP5 models used to calculate the multi-model mean is indicated in the upper right corner of each panel. Hatching indicates regions where the change is small compared to natural internal variability (i.e., less than one standard deviation of natural internal variability in 20-year means). Stippling indicates a large change compared to natural internal variability (i.e., greater than two standard deviations of natural internal variability in 20-year means). Taken from IPCC 2013, Figure SPM 8(a) and (b)<sup>45</sup>. **Right panel:** latitudinal changes in species richness for New World birds. Total species number peaks in tropical regions and falls away towards the poles. Redrawn from Gaston (2000)<sup>152</sup>.

2100 is as “likely as not”, with much greater increases in regional temperatures<sup>45</sup>. Changes in seasonality, precipitation and the frequency of extreme weather events are also predicted, with consequent effects on fire, drought and flood frequency, sea levels, extent of snow pack, stream flows, nutrient availability and soil erosion<sup>45</sup>.

In response to changing temperature and rainfall patterns, species are predicted to shift their geographic ranges, relative abundances and seasonal timings<sup>7,11</sup>. Species differ in their particular climate needs and in their dispersal ability, meaning they will each respond to climate change individually, rather than as communities<sup>11</sup>. Changes in community composition are

predicted to result as species' spatial or temporal associations are disrupted, leading to breakdown of inter-species interactions, such as predation or pollination, and altering competitive balances and ecological networks<sup>7,11,13,46</sup>. Reduction in stability, functionality and productivity of ecosystems may result from changing climatic conditions and, indirectly, from change to or loss of biodiversity, with consequent effects for ecosystem services<sup>47</sup>. Where limits on dispersal ability or natural and human barriers prevent species from shifting their geographic ranges to track suitable climate, extinction has been predicted to result<sup>7,14,15,48</sup>.

Without substantial and sustained reductions of greenhouse gas emissions, the largest amount of warming is yet to come<sup>45</sup>. There is still, therefore, time to plan, evaluate and implement practices and strategies to combat the effects of climate change, preventing biodiversity loss or reducing its impact on ecosystem integrity, function and services<sup>49</sup>. Effective conservation action depends upon accurate and early identification of the species, communities or ecosystems at risk and the appropriate conservation action to take<sup>50</sup>.

The ecological reality and accuracy of current predictions of extinction risk and the methods on which they rely have been questioned<sup>7,30,51</sup>. Estimates of the potential magnitude of climate change-driven extinction risk based on these methods have been alarming; some meta-analyses have suggested that by 2050 15-37% of species will be on an inevitable decline towards extinction for only mid-range warming scenarios, with significantly higher risk for some regions<sup>28</sup>. Such predictions have received intense media attention and have been incorporated into high level policy briefing documents<sup>15</sup> but remain controversial<sup>26,27,29,30,52</sup>.

Methods underlying the majority of current predictions of climate change-driven extinction risk are based on predicted distances that species would be required to move to track their current climatic conditions. Species thought to be unable to shift their geographic ranges to track suitable climates, either due to biological limitations or human and man-made barriers to dispersal, are predicted to suffer elevated extinction risk<sup>14,28,48,53,54</sup>. Evidence from past episodes of warming and from current experiments, models and observations suggests that these methods are not capturing the full range of possible responses. Species have shown abilities to migrate further and faster than current estimates suggest and may show abilities to tolerate unfavourable climatic conditions, or adapt to them<sup>30</sup>. Where species are able to tolerate or adapt to climate change, extinction risk based on range shift alone may be overestimated<sup>7,30</sup>. Conversely, risk may be underestimated if populations within a species are adapted to local conditions, rather than conditions across the species' whole range, or where indirect ecological effects drive vulnerability<sup>7,55,56</sup>.

Predictions of wide-scale species migration and extinction and of the reshuffling of living systems, have led some to ask whether current conservation practices, developed in a pre-climate change context, are up to the task<sup>23</sup>. The effectiveness of traditional conservation strategies, such as restoring or preserving habitats and protecting species within static protected areas, have been called into question<sup>23,57</sup>. Downgrading or declassifying underperforming sites and establishing new reserves in probable movement corridors or regions of net species immigration has been argued to be a more effective use of limited conservation resources<sup>58,59</sup>. Some have suggested that more intensive and invasive practices, such as moving species to locations predicted to have suitable future climates ("assisted migration"), may be the only means of preserving some species under climate change<sup>24,25,49,60</sup>.

To what extent, then, do the potential impacts of climate change demand a re-think of conservation policy, planning and practices? Focusing on terrestrial diversity, this briefing paper will examine past and current responses of species to changed climatic conditions and ask what insights can be gained for the future of biodiversity under climate change. It will discuss current predictions of species' responses to climate change and potential extinction risk, the methods used to generate them and limitations and uncertainties associated with those methods. A new approach, integrated vulnerability assessment, will be discussed which draws on multiple sources of information, including past and current responses to climate change, along with experiments, models and expert assessments, to create a fuller picture of the possible impact of climate change on biodiversity. Finally existing conservation practices will be reviewed in light of climate change and suggestions made for changes that may be necessary to incorporate climate change into conservation policy, planning and practice.

## Current and past responses to climate change

Earth has passed through many episodes of rapid warming and cooling, some very recently on evolutionary timescales (Box 2). Examination of past changes in land mass, ecosystems, community and species distributions and climate, coupled with modern and ancient DNA studies can piece together how species and populations responded to past climate change. Evidence from episodes of rapid warming over the period since the last Ice Age does not suggest the occurrence of species losses at a magnitude comparable with estimates of extinction risk under predicted 21<sup>st</sup> century climate change<sup>61</sup>. Understanding the reasons for this discrepancy is crucial to predicting extinction risk due to future climate change. Evidence from these past episodes of warming suggests that current predictions, based on species' ability, or inability, to track changing climate do not capture the diversity of potential responses, which may include movement to track changing climate (migration), tolerating climate change (persistence) or adapting to it (adaptation) in situ and, for some, local or global extinction (Figure 1).



**Figure 1:** Example population and species-range responses to environmental changes since the last glacial maximum, documented for selected North American conifer trees and Eurasian cervids. Populations of many species have persisted *in situ* at individual sites since the last glacial maximum (persistence) and many have undergone habitat shifts, moving short distances (1 to 10 km) to sites with different aspects, slopes, elevations, and other attributes as the environment changed. Migrations of 100 to 1000 km are well documented for many species. At least a few species have undergone universal extinction (e.g., *Megaloceros giganteus*) owing to environmental change; others have experienced loss of genetic diversity, usually associated with severe population bottlenecks (near-extinction episodes) (e.g., *Picea martinezii*). Species’ responses to climate change may consist of a combination of responses. For example, since the last glacial maximum, populations of *Juniperus osteosperma* and *Alces alces* have persisted at some sites (toleration), undergone habitat shifts (usually elevational or topographic) within some regions, and colonized extensive new territory while disappearing from previously occupied territory (migration). Taken from Dawson et al. (2011), see supplementary material to that paper for further examples and references.

**Migration:** range shifts consistent in direction (i.e. upslope and polewards) with tracking contemporary climate change are already evident across multiple species groups and regions<sup>62-64</sup>. Small scale microhabitat shifts are also occurring<sup>65</sup>. However, for many species, observed range shifts lag behind climate change, suggesting that species may be unable to reach climatically suitable regions, with extinction the predicted result<sup>14,66,67</sup>.

Examination of past responses also reveals evidence of range shifts consistent with tracking changing climate<sup>30,68,69</sup>. However, some species and species groups reached regions that would be impossible based on observed current rates of range shift or estimates of dispersal ability, suggesting that potential rates of migration may be underestimated<sup>30,70,71</sup>. Rare long distance

dispersal (“LDD”) events may enable colonisation of distant locations<sup>70</sup>. Transport of small numbers of seeds, eggs or individual organisms over large distances, for example, by wind, atmospheric updrafts, oceanic currents and streams, or by birds, animals or humans, may establish a species in a new location<sup>30,70</sup>.

LDD may enable species to colonise distant climatically suitable areas, but such events are rare and establishment of populations rarer still, requiring suitable climatic conditions and an available site for colonisation<sup>69,70</sup>. Distance to colonisation site, as well as biological differences between species in reproduction and dispersal, affect the probability of successful colonisation by LDD. Compare, for example, wind-borne seeds with large, flightless and sexually reproducing animals that require two individuals<sup>72,73</sup>.

## Box 2: Climate change past and future

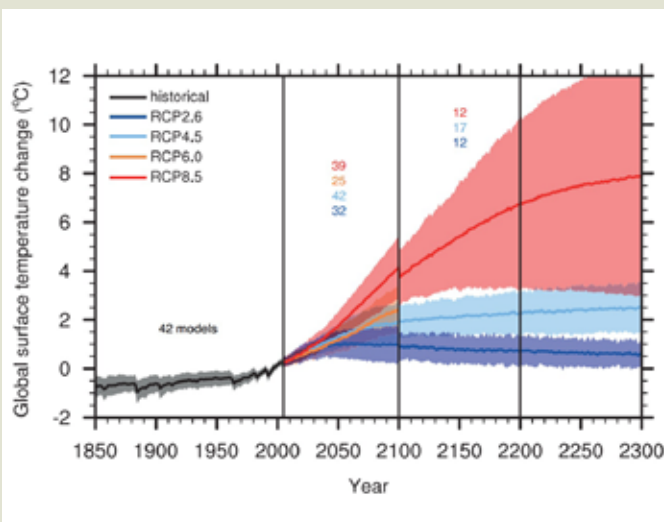
Projected future climate change has been described as unprecedented, both in the rate of change and in its magnitude<sup>154</sup>. The exceptional nature of projected climate change is often stated as one reason for alarming predictions of extinction risk and for radical suggestions for conservation<sup>154,155</sup>. However, can projected climate change really be said to be unprecedented?

When discussing the magnitude and rate of projected future climate change, reference periods used to compare past and predicted rates and magnitudes of climate change are usually narrow, comparing against pre-industrial climate or the climate of the past few thousand years<sup>45,154,156</sup>. These timescales are not relevant to species, the majority of which have been present for many thousands or millions of years<sup>30,34</sup>.

Over the Quaternary Ice Age (approximately the past 2 million years), there have been many individual glacial periods, punctuated by warmer interglacials, like the one we are in now<sup>157</sup>. Ice sheets reached their maximum extent for the most recent of these glacial periods about 21,000 years ago. Each glacial period was punctuated by large and rapid warming (in the North Atlantic region, typically 5–10°C within 50–200 years) and slower cooling events. These events (termed “Dansgaard-Oeschger cycles”) are now known to have had effects extending into the tropics and Southern Hemisphere<sup>45,158</sup>. The subsequent transition to current, interglacial conditions was not smooth. There were a number of minor fluctuations towards colder conditions and one substantial return to cold conditions, with renewed ice sheet formation (“The Younger Dryas” period), terminating in a period of extremely rapid warming about 11,600 years ago. The rates and magnitudes of warming during these past episodes are comparable to projected 21st century warming, with as much as 10°C increase in air temperatures in some mid- to high- latitude regions taking place in fewer than 20 years<sup>159,160</sup>. The causes and the spatial patterns of these rapid warming events were very different from what is happening now, with strong regional patterning<sup>45</sup>. However, even though these events are registered more strongly in some regions than others, biodiversity experiences temperature change at the regional scale; moreover, no region was free of their effects.

Rapid and large magnitude changes in climate are, therefore, not necessarily exceptional. However, past climates and climatic changes are not analogues of predicted future changes. As they took place in glacial periods or during the glacial to interglacial transition, warming started from a cold baseline temperature<sup>157</sup>. CO<sub>2</sub> concentration increased, but as a consequence, not as a cause of the warming. The large and rapid increase in CO<sub>2</sub> that is taking place today has no parallel in the Quaternary period. Atmospheric CO<sub>2</sub> concentration has ecophysiological effects separate from those of global warming, increasing plant water use efficiency and altering the competitive balance between plant species groups using different photosynthetic pathways<sup>161,162</sup>.

Whilst past episodes of warming may have been equally large and equally rapid, what is unprecedented (or at least for current species and species groups) is the expected duration and continuity of climate change. Rapid warming during Dansgaard-Oeschger cycles was followed relatively soon after by slower cooling<sup>158</sup>. Current projections suggest that if emissions are curtailed soon, temperatures will level off. However, they are not expected to decrease for many centuries, and global average temperatures may still reach levels not seen during the last 2 million years (Box 2, Figure 1)<sup>32,45</sup>.



**Figure 1:** Time series of global annual mean surface air temperature anomalies (relative to 1986–2005) from CMIP5 concentration-driven experiments. Time series of global annual mean surface air temperature anomalies (relative to 1986–2005) from CMIP5 concentration-driven experiments. Projections are shown for each RCP for the multi-model mean (solid lines) and the 5 to 95% range ( $\pm 1.64$  standard deviation) across the distribution of individual models (shading). Discontinuities at 2100 are due to different numbers of models performing the extension runs beyond the 21st century and have no physical meaning. Only one ensemble member is used from each model and numbers in the figure indicate the number of different models contributing to the different time periods. No ranges are given for the RCP6.0 projections beyond 2100 as only two models are available. Taken from IPCC 2013, Figure 12.5<sup>45</sup>.

The frequency and magnitude of LDD events is not well predicted from average dispersal distances, instead being quantified from observed rates of range shifts<sup>70,74</sup>. Rates of range shift in response to past episodes of warming may not apply to contemporary climate change, as the landscape over which species will have to move to track changing climatic conditions is radically different from that of the past and human alteration of the landscape may interfere with natural dispersal processes<sup>7,19,25</sup>. As LDD events are rare, the magnitude of contemporary climate change has, so far, been small and the time period over which it has occurred has been short, instances of LDD may be too few to allow quantification of this response in a modern context.

**Persistence:** observed lags in range shift in response to contemporary climate change may, for some species, be indicative of ability to withstand or persist through changed climatic conditions<sup>75</sup>. Evidence suggests that during past episodes of warming, some species may have persisted by being able to tolerate unfavourable conditions, or by escaping them without long distance migration using refugia (localised climate heterogeneity or gaps in the ice sheet) to maintain small populations<sup>76,77</sup>. For example, the Patagonian cypress (*Fitzroya cupressoides*) is thought to have persisted through the last glacial period in at least two refugia in coastal Chile, despite the majority of its current range being climatically unsuitable for tree or forest species<sup>78</sup>.

**Adaptation:** adaptation may be either at the genetic level, by evolution of relevant biological traits, or without genetic change, by phenotypic plasticity<sup>79-82</sup>. Species may be able to reduce the effect of climate change by altering their behaviour, physiology or life cycle timings to reduce the effect of climate change. Evidence that species are showing phenotypically plastic responses to climate change can be found in the many examples of altered timings of breeding, spring emergence, migration dates and flowering associated with changing temperatures<sup>11,62,63 83 84 85</sup>.

Species may be able to respond to climate change at the genetic level (i.e. evolution) within a few generations<sup>80</sup>. Contemporary examples of such rapid adaptive responses are emerging. Pitcher plant mosquitoes (*Wyeomyia smithii*) rely on day length to trigger dormancy. Northern populations have evolved so that entry into dormancy is triggered by shorter day lengths, delaying dormancy and allowing them to take advantage of longer growing seasons under warmer temperatures<sup>86</sup>.

For past episodes of climate change, range shifts were accompanied by the formation of new ecosystems and species communities, suggesting ecological adaptability<sup>87</sup>. Evidence also suggests evolution of dispersal ability accompanying range shift, as individuals from the population with the greatest dispersal ability are most likely to be those establishing new populations<sup>72</sup>. At the end of the last glacial period, Lodgepole Pine (*Pinus contorta*) migrated north into Canada's Yukon Territory from populations south of the ice sheet. Populations at the northernmost edge of the species' distribution show greater

dispersal capability than those at the southern edge, with lower seed mass relative to wing area, allowing seeds to be carried further by wind than their heavier southern counterparts<sup>71</sup>.

Limitations on the extent of adaptive capabilities exist, however. Phenotypic plasticity is programmed by, and may therefore be limited to, the current range of environmental conditions across a species' range. Species may be using the full extent of any plasticity to respond to current climatic variation<sup>56</sup>. Programmed responses may be inappropriate as environmental conditions become more removed from current conditions<sup>88</sup>. Trade-offs and correlations between responses may limit the extent of adaptability<sup>89,90</sup>. Evolution of biological traits affecting vulnerability to climate change may be limited by the degree of genetic variation for those traits, which is likely correlated with conditions recently experienced<sup>91-93</sup>. Relevant traits may not be heritable, so cannot be acted on by evolution<sup>94</sup>.

**Extinction:** to date, there is little evidence of contemporary species extinction that can be attributed solely to recent climate change, if any (but see Pounds et al. (2006)<sup>95</sup>). However, there is evidence of changes in abundance or population declines that may be due to climate change<sup>96-98</sup>. Changes to temperature and rainfall regimes are, as yet, small and habitat loss remains the primary cause of biodiversity loss<sup>3</sup>. Decline or extinction due to climate change is rarely due to the direct effect of changing temperature (though examples do exist<sup>96,99</sup>), but is often due to second order effects, such as changes to habitat type or quality and increase in pests or diseases<sup>55,97</sup>. Consequently, extinction due to climate change is difficult to detect. Declines in abundance, fitness or viability are harder to detect and even harder to attribute to climate change<sup>100</sup>. Lack of contemporary extinctions may suggest that some species are showing a positive adaptive response to contemporary climate change<sup>75</sup>. Conversely, it may suggest an "extinction debt", in which species are on an inescapable path towards extinction but have not yet been pushed over the edge<sup>101</sup>.

Whilst climate change at the last glacial-interglacial transition is not thought to have resulted in extinction on a scale comparable with current predictions of climate-change driven extinction risk, local and global extinctions did occur<sup>61</sup>. Some species increased in abundance and were able to expand their ranges rapidly when conditions were favourable<sup>69</sup>, whilst others underwent severe reductions in abundance or, ultimately extinction<sup>102-104</sup>. For trees, at least one species, *Picea critchfieldii*, is known to have become extinct<sup>105</sup>. Many species of large mammals, such as mammoths, also became extinct<sup>8,104</sup>.

## Lessons for conservation in a climate change context

Evidence for low levels of extinction at the last glacial-interglacial transition and evidence of diversity in past and contemporary responses to climate change should not, however, be interpreted

as meaning that current climate change is not a threat to biodiversity and that species will simply cope. The extent to which migration, persistence or adaptation may buffer or prevent extinction risk for contemporary species is unknown and limitations to these mechanisms exist<sup>30</sup>.

Future climate change will take place in the context of truly unprecedented levels of human influence, with vast portions of the Earth's surface converted to human use, and stresses such as over-exploitation, invasive species, pollution and nutrient loading acting in concert with climate change<sup>7</sup>. Evidence from past and current responses suggest that multiple threats acting simultaneously, and potentially synergistically, may be a deadly cocktail driving species towards extinction and altering ecosystems<sup>8,9,95</sup>. Extinction of many species of large mammals at the end of the last glacial period may be due neither to climate change nor the arrival of humans alone but, perhaps, the combination of both<sup>8,106</sup>.

That many species alive today have passed through multiple episodes of rapid and large magnitude warming suggests that climate change is not, perhaps, a new and unprecedented threat to biodiversity. However, it is a new and unprecedented threat in the context of current landscape use and conservation practices, which were developed in a pre-climate change context<sup>25</sup>. The main cause of biodiversity loss during the recent past and for today is not climate change but land-use change<sup>3,12</sup>. Threat from land-use change, over exploitation, pollution and invasive alien species tends to be more tightly focused in particular regions or on particular species groups<sup>3,12,107,108</sup>. Consequently, conservation has often concentrated on threat reduction, for example by creating reserves to protect species and habitats.

Climate change differs from other threats in the pervasive nature and global scale of its impacts, potentially affecting gene frequencies, population and species abundances and distributions, the structure of communities and ecological networks, and the distribution of ecosystems and biomes<sup>7,12,13,80</sup>. All species and regions may be impacted by climate change, to varying extents. What is more, they potentially represent shifting targets for conservation, with climate change moving species relative to static reserves<sup>109,110</sup>. Differences between climate change and other threats suggest that a "business as usual" approach to conservation practice is unlikely to lead to effective conservation in changing climatic conditions. Climate change will undoubtedly require a conservation response but how species, regions or ecosystems that are at greatest risk should be identified, and what action should be taken to take to protect them, remain key questions.

## Predicting extinction risk from climate change

Current predictions for possible levels of extinction risk are mostly based on a very narrow method base, termed species distribution modelling (SDM) or climate envelope modelling<sup>30</sup>. The current climatic conditions across a species' geographic distribution are used to define an 'envelope' of suitable climate. Potential

future geographic ranges are identified as regions falling within this envelope for future climates. The fate of the species is then predicted by comparing the size and degree of overlap of these regions with the current species' geographic range and possible species' dispersal scenarios<sup>14,28,48,53</sup>.

SDMs assume species' current geographic ranges to be defined by climate and close correlates of local climate. In reality, geographic ranges are dynamic, with constant changes to range edges and abundances across the range. Ranges represent a balance between the effect of climatic and other environmental conditions on multiple factors. These include population demographic processes (recruitment and local extinction) and physical barriers to species movements (e.g. mountains, roads) or interactions with other species (such as competition, predation) that may prevent them from reaching or surviving in all locations that are climatically suitable<sup>111-113</sup>. Statistical relationships between species' current geographic distributions and climate variables are likely to be poorly predictive of future ranges as climatic conditions move further away from those recently experienced and include novel combinations of climatic variables<sup>114</sup>. Predictions are affected by the scale at which the analysis is conducted. Smaller grid sizes catch topographic heterogeneity (relief, terrain and landscape features) and small scale variations in habitat that are averaged away at larger scales. The ability of microhabitat and microclimate to buffer the impact of climate change may be underestimated, and dispersal required to track suitable climates may, consequently, be overestimated in areas of high topographic diversity<sup>115</sup>. Conversely, SDM may overestimate climatic tolerances, potentially underestimating risk, where there is limited gene flow between discrete populations that are locally adapted to climatic conditions<sup>56,79</sup>.

SDMs largely measure species exposure to climate change, which is the magnitude and nature of climate change predicted to occur in regions where a species is currently present. Exposure is only one factor affecting probability of decline or extinction, 'vulnerability', to climate change. Differences between species in their ecology, physiology, anatomy and life history will affect vulnerability by determining differences in their ability to tolerate change, 'sensitivity', or their adaptive capacity<sup>19,30</sup> (Box 3). Predictions from SDMs do not account for the diversity of species' responses and their potential resilience to climate change, as in past and current episodes of climate change. Nor do they account for the potential of biological differences between species or ecological feedbacks to increase vulnerability<sup>19,30</sup>.

## Integrated vulnerability assessment

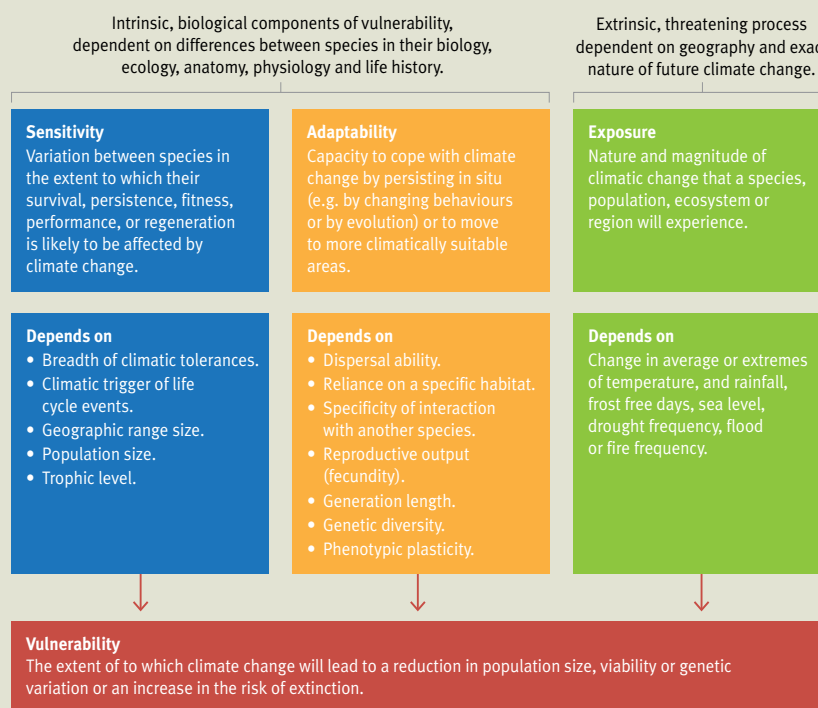
More accurate predictions of climate change impacts and better options for management will result from shifting focus away from simple range shifts and towards an integrated approach to climate change vulnerability assessment, in which multiple sources of information are evaluated for the full range of possible species' responses<sup>30</sup>. Examples of these approaches are starting to appear in the literature, as are studies identifying traits that may impact sensitivity or adaptive capacity (see Box 3)<sup>17,19,21</sup>.



### Box 3: Sensitivity, adaptive capacity in vulnerability assessment: the importance of biological differences in extinction risk

Responses and extinction risk due to climate change will depend on more than exposure alone. Species' responses will be mediated by differences in their biological characteristics that will affect their ability to withstand climate change ('sensitivity') or adapt to it ('adaptive capacity') (Box 3 Figure 1)<sup>30</sup>. A combination of expert assessment and modelling methods is beginning to identify traits that affect sensitivity and adaptive capacity for climate change<sup>19,21</sup>. Traits that are associated with high sensitivity and/or low adaptive capacity,

so high vulnerability to climate change, appear to have some overlap with traits already targeted by current criterion-based conservation prioritisation frameworks, such as the IUCN Red List<sup>21</sup>, suggesting possible synergy between sensitivities to threats. The type and timing of responses will depend on the balance of sensitivity, adaptability and exposure to climate change. The Patagonian cypress is a long lived (c. 3000 years) species with poor dispersal capacity, traits which favoured its persistence in refugia instead of migration to track changing climate<sup>78</sup>. In contrast, Lodgepole Pine has wind dispersed seeds, favouring rapid range shift to track changing climatic conditions<sup>71</sup>.

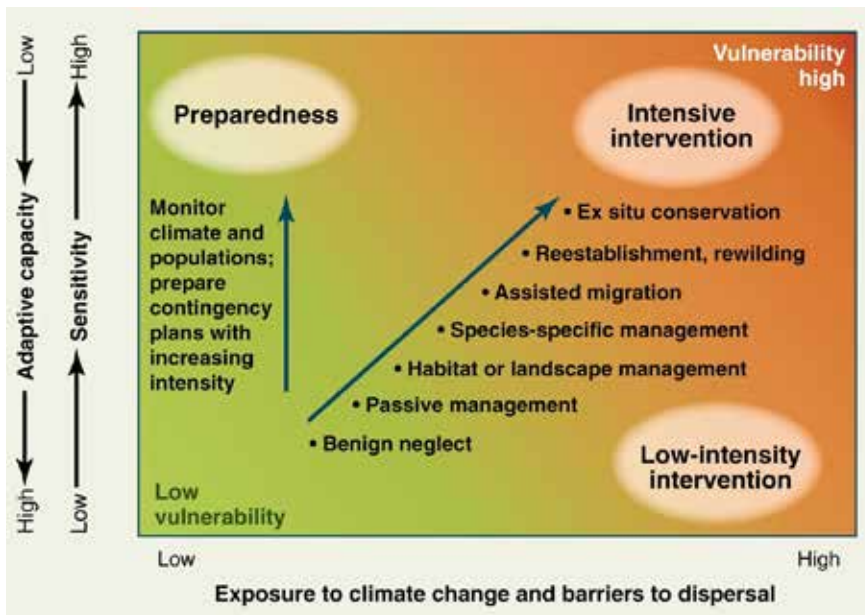


**Figure 1:** Sensitivity, adaptive capacity and exposure in vulnerability assessment. Responses to climate change will be mediated by species biology, which may increase or decrease vulnerability for a given amount of exposure by affecting sensitivity and/or adaptive capacity. Specific climatic requirements, such as reliance on rainfall to trigger breeding, are likely to increase sensitivity. Reliance on a particular species interaction, such as reliance by a plant on pollination by a particular insect, may increase sensitivity of that plant if the pollinating insect is climate change sensitive, and may also reduce adaptive capacity by preventing range shift without the same shift by the pollinator. Differences in dispersal capabilities and reproductive capacity may affect whether species can reach new climatically suitable regions and establish viable populations. Ultimately, vulnerability will depend on the combination of sensitivity, exposure and adaptive capacity of species to climate change and other anthropogenic threats.

Whilst we have largely discussed species vulnerability, integrated frameworks are equally applicable to any aspect of biodiversity. Ecosystem vulnerability could be assessed in terms of the sensitivity of flood or fire regimes, by examining the sensitivity of individual component species, or of ecologically relevant groups of species, for example those with key functional traits for ecosystem services<sup>33,116</sup>.

Integrated vulnerability assessment will also inform conservation planning. Which strategy is most appropriate and how urgent is the need for intervention will depend on the relative balance of sensitivity, exposure and adaptive capacity (Figure 2). Where

vulnerability is low, it may be that little action is urgently required and that low level monitoring is sufficient. For highly vulnerable species or systems, immediate and intensive intervention may be necessary, such as assisted migration or ex situ conservation in breeding programs or seed banks<sup>30</sup>. Where exposure to climate change is low but sensitivity is high or adaptive capacity is low, more intense monitoring with contingency plans may be required. Highly adaptive species or ecosystems may benefit from increasing connectivity or landscape permeability to facilitate dispersal, or population management to facilitate adaptation. Highly sensitive systems may need actions to promote resilience, such as designating new reserves, restoring habitat and



**Figure 2:** Vulnerability-based conservation strategies. The two axes shown split vulnerability into intrinsic biological components (sensitivity and adaptive capacity) and external geographical components, namely exposure to climate change. Where a species or ecosystem falls between these axes will help in deciding what conservation strategy to apply and how urgently intervention may be needed. Taken from Dawson et al. (2011)<sup>30</sup>.

reducing the impact of other threats. Individual species with high sensitivity or with high impacts on ecosystem sensitivity or function, such as specialist pollinators, may require more intensive targeting<sup>30,117</sup>.

### Management choices and planning frameworks for climate change conservation

Because it is such a different kind of threat, climate change is prompting conservation practitioners to look again at the aims, principles and objectives of their plans. Many of the practices upon which managers currently rely will continue to be relevant and useful in a climate change context, especially because other threats to species, such as land-use change, are still important. However, changes may need to be made that acknowledge the rapidly changing nature of the environment, the way that species may respond and the consequent effects upon ecosystems and ecosystem services.

**Embrace change:** climate change, coupled with increasing appropriation of land and resources by a growing human population, may mean it is unfeasible to preserve some species, communities and ecosystems as they are and in the geographical locations in which they currently exist<sup>33,114,118</sup>. Novel interactions, communities and ecosystems will become more common as climate and other anthropogenic change intensifies. In reality, there is nothing novel about novel ecosystems. Today's natural systems are the novel ecosystem of the past<sup>87</sup>. The distinction between "natural" or altered systems is often subjective and depends on the time frame applied<sup>57,119</sup>. Climate change (past and present), loss of biodiversity, nitrogen deposition, land-use change, invasive species, release of pollutants and resource exploitation have wide-scale and far-reaching effects<sup>3,57,120</sup>. Just as past climate change created new interactions and communities, future climate change is predicted to do so<sup>87</sup>, and may already be doing so where species have shifted their ranges, life cycle timings and habitats in response to climate change<sup>11,13</sup>.

Embracing change does not, however, mean embracing all change. Accepting new species' arrivals or novel communities without question is unlikely to be the best strategy for maintaining global or local biodiversity. A balance between potentially opposing flexible and precautionary approaches is required<sup>57,119</sup>. New species' arrivals (whether naturally or human introduced) may need a cost/benefit analysis on a case by case basis<sup>121,122</sup>. A native species/alien species dichotomy may cease to be useful<sup>32</sup>. Where transition of an ecosystem to a new state seems probable, managers should consider whether the transition is inevitable and, where it can feasibly be prevented, if permitting or assisting that transition may in the end be more desirable or practical. The degree of human or climate change impact on a system, the feasibility or cost implications of maintaining the historical ecosystem, the resilience or stability of the novel system, and its capability to provide necessary ecosystem goods and services are all relevant considerations and will inform decisions as to desired outcome and management strategy<sup>118,119</sup>.

Change must be factored into conservation objectives and strategy choices. Management to promote continued functioning and viability of ecosystems or populations in changing climatic conditions, or within novel ecosystems, may be a more feasible objective than preserving past systems<sup>57</sup>. There might reasonably be less concern about changes in species' identities as long as functions, such as pollination or primary production, are maintained<sup>33,34</sup>. Interventions aimed at preserving habitats or ecosystems and preventing change may, in some cases, have to be swapped for those promoting the ability of a species or ecosystem to adapt to changing climate, such as enhancing connectivity and permeability of the landscape<sup>32-34,123</sup>.

**Accept uncertainty:** uncertainty in projections of future climate may be largely irreducible, given the contingent nature of processes driving climate change<sup>35</sup>. Uncertainty must, therefore, be incorporated into conservation planning and practice through

flexible decision-making frameworks, such as scenario planning and adaptive management (Figure 3).

Scenario planning requires a flexible approach to setting conservation goals. Rather than setting management goals for a predicted future climate or ecosystem state, scenario planning involves using climate models to explore the costs and benefits of management actions under a range of plausible climatic and ecological futures<sup>35</sup>. Such exploration may identify “win-win” interventions that are robust to climate, delivering desired outcomes under a range of future climates, and also those that fail to deliver in all future scenarios<sup>33,35</sup>. It may also lead managers to set multiple goals, if differences between scenarios are so great that a single goal is unachievable<sup>124</sup>. Translating scenario planning into effective management requires monitoring of the target species or system, and the environmental conditions that may be driving any observed change, to identify which scenario is being most closely played out<sup>33</sup>.

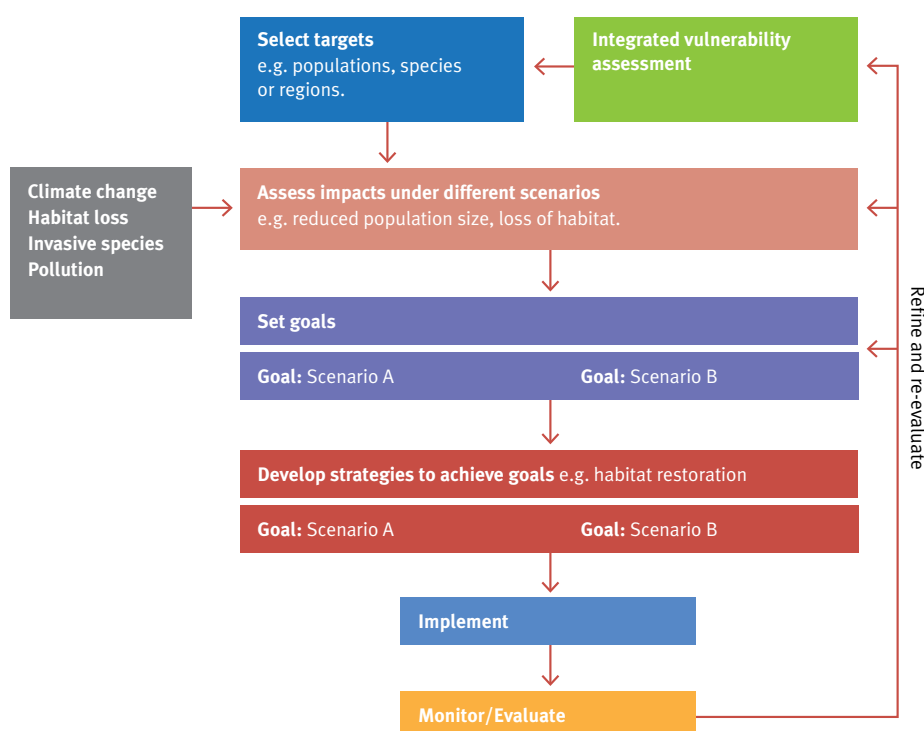
Adaptive management involves an iterative approach, where actions are monitored and continually re-evaluated, with changes being made where necessary. It is a learning process, but can vary in the degree of active learning it involves. At the basic level, the consequences of interventions are monitored and fed back into the decision-making process. At the other end of the spectrum, a range of interventions could be implemented as experiments to actively and empirically evaluate whether, and in what contexts, they are effective. This flexible and adaptive approach allows management in uncertain situations<sup>30-33</sup>.

That management should be adaptive is not a new proposal, but uptake of such practices by managers has been low<sup>125</sup>. Diverting limited conservation resources to monitoring may seem a less effective application of those resources than direct conservation actions. Given the uncertain future faced by biodiversity under climate change, application of adaptive management and scenario-planning frameworks is crucial to understanding and predicting the impacts of climate change and to minimising biodiversity loss. However, it may require a fundamental shift in how conservation funds are allocated<sup>30-33</sup>.

### Protected areas under climate change

Despite the potential for large-scale species migration, reserves should remain a principal component of conservation strategy under climate change. Existing reserves will act to protect high quality habitat, buffering extinction risk, as well as facilitating persistence and providing suitable regions for colonising species or stepping stones for shifting species<sup>32,126,127</sup>. Models and observations suggest that although the identities and relative abundances of species within reserves are expected to change, reserves may remain centres of high species diversity<sup>126-128</sup>. Migrating species may show preferential colonisation of protected over non-protected areas, meaning movements out of reserves could be, to some extent, countered by an influx of colonists<sup>126-128</sup>.

Threat reduction will continue to be crucial for supporting resilience and adaptive capacity. Reducing stress on a population



**Figure 3:** Conservation decision making in a climate of uncertainty. Management in a climate change context may require a flexible and iterative approach. Ongoing outputs from conservation interventions feedback to improve and refine vulnerability assessments, increase understanding of the impacts of threat, and inform managers as to the effectiveness of interventions and likely scenarios. Adapted with modifications from Bellard et al. (2012).

or ecosystem by decreasing the impact of invasive species, habitat loss, or exploitation may result in larger populations that are better able to absorb climate change, are more viable and are more phenotypically or genetically varied<sup>31,117,129</sup>. Restoration of damaged ecosystems will provide some important insurance in an uncertain climate by increasing stability and promoting resistance or resilience<sup>33,119</sup>. However, focus could shift from recreation of historical species groups to recovery of processes that promote habitat or ecosystem integrity, such as disturbance regimes and river or stream flows<sup>33,34</sup>.

If reserves are to remain a key conservation tool, climate change needs to be factored into any evaluation and expansion of the protected area network. Given the potential for large geographic species movements, a holistic approach must be applied, examining individual protected areas as part of a network of coverage<sup>31</sup>. Identifying key regions to plug gaps in coverage or improving landscape connectivity may increase adaptive capacity and boost resilience, both by facilitating species' movements and by increasing the area and diversity of available habitats<sup>130</sup>.

SDMs have been used to examine performance of current reserves under climate change<sup>109,110,127</sup>, to identify potential movement corridors<sup>131</sup> and to identify regions required to protect species' future geographic distributions<sup>132</sup>. These methods rely heavily on the ability to predict future climate and species' geographic ranges, both of which are uncertain<sup>33</sup>. Instead of species-driven landscape planning, preserving a diversity of environments (habitat, geology, topography, soil, hydrology) may preserve a large number of species by providing a range of suitable conditions<sup>133–135</sup>. Similarly, protecting regions where species have high evolutionary potential, or where high topographic or habitat diversity may promote species persistence, migration and adaptation, may increase ecosystem resilience or adaptive capacity by preserving the processes that generate biodiversity<sup>31,33,34,129,133</sup>.

Accepting that species may shift their geographic ranges to track changing climate, concentrating landscape conservation within reserves may leave large areas of inhospitable terrain for moving and colonising species. Landscape management outside of reserves could facilitate dispersal by increasing permeability and including habitat mosaics within the wider landscape<sup>34,123</sup>. This should allow species to pass through the landscape and provide more sites for them to persist, increasing resilience and adaptive capacity<sup>32,123</sup>. Examples of species persistence in small isolated populations in an otherwise hostile landscape during past warming are evidence that even small patches of intact habitat may be crucial to persistence through climate change<sup>34</sup>. A mosaic of land uses and less damaging landscape practices, such as low intensity forestry, may provide some opportunity for persistence or migration<sup>31–33</sup>. Enhancing existing linear features, such as rivers, hedgerows and embankments may improve connectedness without actively creating new corridors<sup>123</sup>.

## Assisted migration in species conservation under climate change

Observed rates in species' range shifts are thought to be too low relative to the expected rates of climate change to allow species to track their current climate by dispersal. This observed dispersal deficit has led to calls for assisted migration (also termed assisted colonisation or translocation), which involves artificially increasing dispersal by actively moving species from their current locations to regions predicted to be climatically suitable<sup>24,25</sup>. Assisted migration, however, remains a controversial strategy for several reasons.

Of greatest concern is the creation of new pest or disease problems attributable to the migrants at the site of introduction, with deleterious consequences for native species and consequent ecosystem effects<sup>24,136</sup>. Those in favour of assisted migration argue that the risks are limited if assisted species movements are well planned and are of the right species into the right locations. Movements within biogeographic regions (regions sharing broadly similar sets of organisms, geographical and environmental features) rather than between continents, or introduction of species into regions with no or few endemics and large numbers of generalist species (Britain, for example), are argued to be lower risk<sup>24,25</sup>. However, many examples exist of past species introductions that have had disastrous consequences, even when such introductions were intentional, well-planned and researched, suggesting that results are unpredictable with indirect and unforeseeable ecological knock-on effects<sup>136</sup>. Others argue that change is inevitable and the creation of "unnatural" communities is not a relevant consideration in the context of climate change and extensive human modification of environments<sup>25,57</sup>.

Proponents of assisted migration also argue that risks need to be balanced against the possibility that, for some species at least, it may be the only solution. Species occupying single lakes, islands or isolated mountain tops, or surrounded by environments through which they cannot disperse, may be unable to reach new climatically suitable regions<sup>25</sup>. For example, the Quino checkerspot butterfly (*Euphydryas editha quino*), a native of Mexico and California, has shifted its geographic range in response to climate change (upslope and to higher latitudes)<sup>11</sup>, but is blocked from future climatically suitable regions by a substantial and, in all likelihood, insurmountable barrier, Los Angeles<sup>137,138</sup>. Decision frameworks balancing the risks and possible benefits of assisted migration against the likely effectiveness of other, less intensive interventions are emerging<sup>24,60</sup>. However, decisions will have to be made on a case-by-case basis and assisted migration is likely to remain one strategy of last resort<sup>32</sup>.

Translocation of individuals within the existing (or recent historical) geographic range of a species is, by contrast, not a particularly controversial practice. Recently locally extinct species have been re-established or individuals have been moved between populations to improve viability. For example, pumas (*Puma concolor stanleyana*) were introduced into a remnant population of Florida panthers, a closely-related subspecies

(*Puma concolor coryi*), to combat low genetic variability, male sterility and heart defects<sup>139,140</sup>. Translocations could equivalently be used to facilitate species range shifts, for example, by introducing individuals with warm-adaptations to a poleward range edge or to boost variability of colonising populations at the genetic level. Detailed risk assessment and planning would still be needed, as warm-adapted individuals may have a competitive advantage in a changing environment<sup>141,142</sup>, or may hamper evolution of other adaptive traits, such as dispersal capability<sup>143</sup>.

Whilst the debate on assisted migration has largely focused on the risks and benefits for species conservation, potential impacts for ecosystem function are also relevant. If management is to be more focused on ecosystem resilience or function, decisions to move individual species may need to be considered in the context of their impact on the target system. For example, moving a species only if it will carry out a desired function within the ecosystem, such as the introduction of an ecologically equivalent species to replace an extinct one<sup>24,25</sup>.

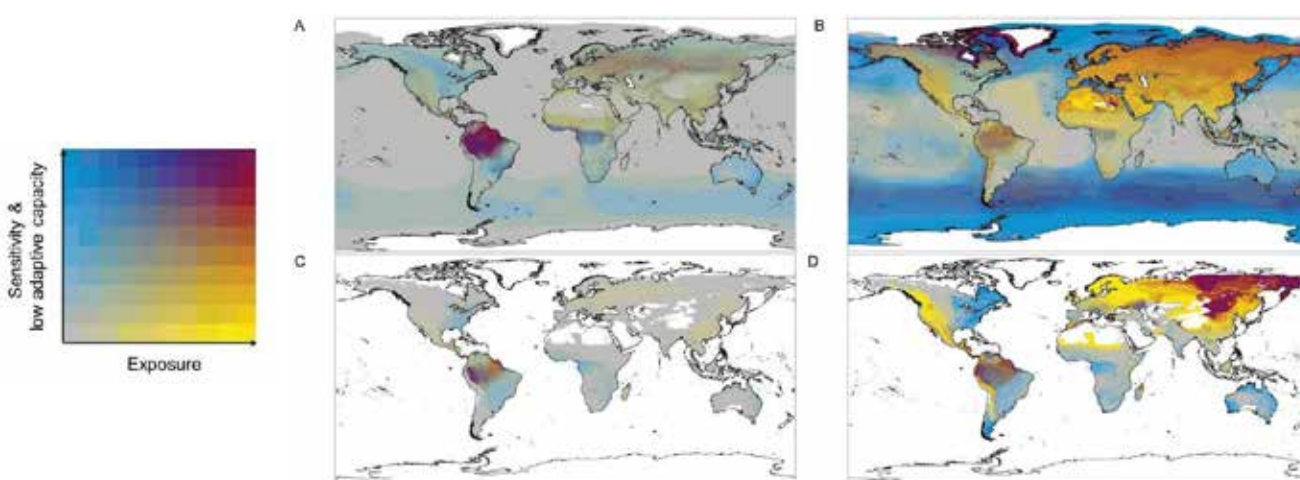
### Global approach to climate change conservation policy and practice

A new attitude may be needed, not only for designing interventions and setting conservation goals, but for conservation policy, practice, and supporting and enacting legislation. These are often very regionally or nationally focused. As climate changes, species will not be limited by human boundaries and may move into and colonise regions outside those considered to be their natural locations. Climate migrants may cause reductions in abundances and range sizes, or even extinction, of native species. Whether conservation policy continues to protect natives and eradicate so-called alien species is an issue going to the

heart the new perspective that climate change may require<sup>121</sup>. If maintaining total global biodiversity is the objective, species that shift across political, legislative or administrative boundaries to track climate should not necessarily be treated as undesirable, even if they have negative impacts for some “native” resident species and create novel interactions or ecosystems<sup>32,57,110</sup>.

Reserves are expected to play a crucial role in buffering species from extinction risk due to climate change and land use change, but may no longer protect the species for which they were designated. Embracing changing ecosystems may need supporting legislative and policy changes, with a more unified and global approach to protection and better coordination between scientists, land managers and conservation organisations<sup>31,32</sup>. Federal, national and site or species-specific thresholds or criteria for protection may hinder effective conservation where broad scale geographic movements are anticipated<sup>32,127</sup>.

Broad scale geographic patterns in biodiversity and climate change also demand greater cooperation and coordination by governments, policy makers and conservation managers beyond the national level. Climate change vulnerable species may be concentrated in tropical regions, as exposure, sensitivity and adaptive capacity are not geographically uniformly distributed<sup>17,19</sup> (Figure 4 and Box 1). Significant conversion of natural habitat to agriculture and deforestation is predicted to be greater in tropical regions compared to temperate zones, as their economies develop<sup>5</sup>. Climate change and land-use change, acting alone and together, may make tropical regions a priority for conservation<sup>16,17,19,144</sup>. However, detailed vulnerability assessment and conservation planning in the tropics are hampered by the bias in expertise, data availability and resources towards species in temperate zones<sup>16,22</sup>.



**Figure 4:** Geographical patterns in vulnerability. Maps show total numbers of climate change vulnerable birds (A) and amphibians (C) and proportions of climate change vulnerable birds (B) and amphibians (D) in a region. Blue regions are those with concentrations of sensitive and poorly adapting species. Yellow regions are those with concentrations of exposed species. Maroon regions are those with concentrations of sensitive, poorly adapting species and exposed species, and correspond to areas of high climate change vulnerability. Colour intensity increases with increasing number/proportion of birds and amphibians. Grey areas have low concentrations of amphibians or birds. Proportions of vulnerable species may be greater at higher latitudes, as fewer species live in these regions. However, total numbers of vulnerable species are greatest in tropical latitudes. These maps were based on a moderate (A1B) emissions scenario for 2050. Taken from Foden et al. (2013)<sup>19</sup>.

Tropical regions are generally in low income countries that can afford neither the cost of establishment of protected areas nor the opportunity cost of impeding development for the sake of biodiversity protection. Schemes such as REDD (Reducing Emissions from Degradation and Deforestation<sup>145</sup>), REDD+ (which includes conservation, sustainable forest management and enhancement of forest carbon) and payments for ecosystem services may go some way to addressing this issue. However, financial and other support from wealthier nations is likely to be necessary in assisting tropical countries to protect and preserve biodiversity, whilst developing sustainably<sup>16,146,147</sup>.

## Knowledge gaps and key areas for future research

There is growing consensus that SDMs alone are not a sufficient basis for species-level conservation prioritisation<sup>7,30</sup>. Integrated vulnerability assessment in a climate change context may provide a more robust and informative alternative, but is an emerging science. Evidence of past and current movements, adaptations and examples of persistence and extinction provide only the starting point. Basic data on biological and ecological traits that mediate vulnerability to climate change is lacking for most species or living systems. Greater understanding of how these traits mediate vulnerability and determine responses, and in what context, is needed in order to predict the consequences of climate change for biodiversity<sup>30</sup>. However, there is also an urgent need for early, preventative action to protect and preserve biodiversity now, and uncertainty is not a reason to delay acting<sup>50</sup>. Wider application of scenario planning approaches is required to identify interventions that may be robust to climate change, allowing managers to take action now that will be beneficial under climate change as well<sup>35</sup>.

A growing number of observations and models show that responses are often complex<sup>37,46,148–150</sup>. Species' responses rarely correspond directly to a change in mean temperature or rainfall, but rather to local or indirect effects of climate change<sup>55</sup>. Vulnerability will be mediated not only by how the biology of the individual species determines its sensitivity and adaptability to climate change, but by the sensitivity and adaptability of species with which it interacts<sup>19,75</sup>. Ecological states and species' geographic ranges or abundances are often the product of hard to predict processes and mechanisms, such as interactions between climatic variability, habitat disturbance and population colonisation, local extinction and persistence<sup>69,151</sup>. Greater understanding of these processes and mechanisms, potential ecological feedbacks and indirect effects of climate change is urgently needed to improve predictions of climate change impacts on biodiversity.

Some species may be capable of adapting to climate change through evolution or plasticity, but the degree of genetic variability or plasticity in traits that may affect sensitivity or adaptive capacity is unknown, as is the extent to which adaptability may buffer extinction risk. What evidence there is suggests that the rate and extent of adaptive capacity is limited relative to the predicted rate and magnitude of climate change, but with

great variation among species<sup>30,75,80,88,92,94</sup>. A strong body of theory suggests that responses will be linked to correlations between environment and fitness, shaped by a species' recent evolutionary history<sup>79</sup>. Consequently, plasticity and genetic variability may be limited by local adaptation or the extent of historical climatic variability<sup>56,92</sup>. Research is underway to identify indicators and to develop models of adaptability and its limits in a climate change context, but is still developing<sup>75,79</sup>.

The prevalence of geographic range shifts associated with past episodes of warming and cooling suggests that movement to track climate will be the primary response of a large number of contemporary species<sup>68</sup>. However, dispersal distances for the majority of species are poorly documented. While theoretical exploration of the potential impact of LDD suggests it may have a major role in driving range shifts<sup>74</sup>, quantification of the frequency with which LDD events occur and distances involved, or of any regional or species-level variability in LDD and the likely effect on future range shifts is lacking.

Individual species and ecosystems may respond differently where they are exposed to multiple stresses. Models have been used to explore the potential for habitat loss to exacerbate the effect of climate change<sup>9</sup> and evidence from past extinctions of large mammals suggests that climate change and human hunting may have acted together<sup>8,106</sup>. Land-use change is still, and will remain for some time, the primary threat to biodiversity but understanding of the interaction between climate change and other threats remains largely theoretical, with little observational evidence from contemporary systems to inform or test model conclusions.

Perhaps most importantly, climate change is a new threat in a conservation context and there is still much to learn. It has not yet been substantially incorporated into conservation planning and practice and there is little evidence for the effectiveness of strategies in reducing the impact of climate change on biodiversity. Evidence of the application of conservation practices and the contexts in which they have succeeded or failed will be the key to successful application of adaptive management and scenario planning. The possible impact of biological traits on sensitivity and adaptive capacity, and the potential outcomes of conservation interventions, can be explored through experimentation and modelling. However, information from real systems and species is needed to test conclusions from models or experiments. Data collection as part of ongoing monitoring and evaluation within a scenario planning and adaptive management framework will be a key source of information for construction and validation of models, and will assist in filling out the framework for integrated and adaptive approaches to conservation. Monitoring and continual re-evaluation of actions and their impacts will shift focus from documenting extinction to identifying and quantifying declines, shifts in abundance and changes to population or ecosystem viability or functioning in real time. These outputs will, in turn, inform long term planning by increasing understanding of climate change impacts on biodiversity and the effectiveness of interventions.

## Conclusions and recommendations

Climate change and pressures from land-use change and habitat degradation, exploitation of natural resources for food, timber and other products, pollution and invasive species are anticipated to intensify as the human population grows. These stresses, acting separately and together on species, communities and ecosystems, are depleting and will continue to deplete biodiversity. Consequently, they will reduce the stability, functional efficiency and productivity of ecosystems, with effects on ecosystem goods and services.

Evidence from past and current climate change, models and experiments suggests species' responses to climate change will be diverse. For some species, there will be greater resilience to climate change than predictions based on range shifts suggest. For others, biological traits, indirect ecological feedbacks or local adaptation may increase vulnerability relative to range shift predictions. The extent to which diversity in responses may buffer and protect species from extinction risk is, as yet, unclear. Land-use change and other anthropogenic threats currently acting to reduce population sizes and viabilities may mean that biodiversity is less resilient to climate change than during past episodes of climate change. What is clear is that responses to climate change will be more complex, and predicted responses to climate change will be more uncertain, than is suggested by methods based on range shifts alone.

Conservation policy and planning under climate change may need to apply new perspectives to traditional conservation practices.

- **Embrace change:** effective conservation policy and practice may, in many cases, be required to accept some change rather than aiming to preserve existing ecosystems with their current component species, as climate change and other pressures from a growing human population make ecological change in many regions and natural systems inevitable.
- **Global approach:** distinctions between native and non-native species may become less relevant as species shift their geographic ranges. Global rather than regional or national targets or criteria for species or habitat protection or designation of protected areas may be more appropriate as species' ranges and abundances change. Focus may need to shift towards preventing net global biodiversity loss instead of preserving current species groups and ecosystems.
- **Function approach:** focus on ecosystem function and resilience may be more appropriate than on maintaining species community composition. Traditional practices, such as protecting or restoring habitat within reserves, may support function and resilience by allowing existing systems to absorb the impacts of climate change. Improving permeability of the landscape or connectedness between reserves may be required to facilitate range shifts, either through spatial structuring of new reserves or by enhancement of natural linear features, such as rivers and hedgerows.

Decision-makers and managers must accept that uncertainty as to future climate may be, to some extent, irreducible. Uncertainty must, therefore, be incorporated into decision frameworks and interventions through adaptive management and scenario planning. Ongoing monitoring as part of this flexible management approach will assist conservation of the target system or species. It will also increase understanding of climate change impacts on biodiversity and of the effectiveness of conservation strategies, feeding back into vulnerability assessments and conservation planning to improve predictions.

Identification of regions, ecosystems and species likely to be highly vulnerable to climate change requires an integrated approach, in which all available sources of information are included in a single framework. Integrated approaches may provide a biologically detailed and informative assessment of vulnerability and may identify traits, processes or additional threats contributing to vulnerability. These approaches will also assist strategy choice, as the balance of sensitivity, adaptive capacity and exposure will influence the nature of potential interventions and the urgency with which they are required.

Early applications of integrated vulnerability frameworks suggest that tropical regions may be centres of climate change vulnerability. Climate change, coupled with predicted increases in land-use change in these regions, suggests that tropical zones may be future centres of biodiversity loss. Stemming loss is likely to require a co-ordinated international response, with transfer of expertise and financial assistance from high-income developed temperate nations to assist low-income tropical nations in increasing their level of human societal development in a sustainable manner.

## Acknowledgements

The authors gratefully acknowledge Brian Huntley, Rob Ewers, Joshua Lawler and Stephen Jackson for reviewing the manuscript, and Simon Buckle for editing and technical contributions.

## References

- Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: Biodiversity Synthesis*. (Island Press, 2005).
- Dirzo, R. *et al.* Defaunation in the Anthropocene. *Science (80-)*. **345**, 401–406 (2014).
- Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: Current State and Trends*. (2005).
- Carpenter, S. R. *et al.* Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. *Proc. Natl. Acad. Sci.* **106**, 1305–1312 (2009).
- Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: Scenarios Assessment*. (Island Press, 2005).
- Pereira, H. M., Navarro, L. M. & Martins, I. S. Global biodiversity change: the bad, the good, and the unknown. *Annu. Rev. Environ. Resour.* **37**, 25–50 (2012).
- IPCC. *Climate Change 2014: Impacts, Adaptation, and Vulnerability Working Group II Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (Cambridge: Cambridge University Press, 2014).
- Lister, A. M. & Stuart, A. J. The impact of climate change on large mammal distribution and extinction: evidence from the last glacial/interglacial transition. *Comptes Rendus Geosci.* **340**, 615–620 (2008).
- Travis, J. M. J. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. R. Soc. London. Ser. B Biol. Sci.* **270**, 467–473 (2003).
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365–377 (2012).
- Parmesan, C. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).
- Pereira, H. M. *et al.* Scenarios for global biodiversity in the 21st Century. *Science (80-)*. **330**, 1496–1501 (2010).
- Walther, G.-R. Community and ecosystem responses to recent climate change. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2019–2024 (2010).
- Loarie, S. R. *et al.* The velocity of climate change. *Nature* **462**, 1052–1055 (2009).
- Fischlin, A. *et al.* in *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. (Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J. & Hanson, C. E.) (Cambridge University Press, 2007).
- Lee, T. M. & Jetz, W. Future battlegrounds for conservation under global change. *Proc. R. Soc. B Biol. Sci.* **275**, 1261–1270 (2008).
- Dickinson, M. G., Orme, C. D. L., Suttle, K. B. & Mace, G. M. Separating sensitivity from exposure in assessing extinction risk from climate change. *Sci. Rep.* **4**, 6898 (2014).
- Deutsch, C. A. *et al.* Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci.* **105**, 6668–6672 (2008).
- Foden, W. B. *et al.* Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS One* **8**, e65427 (2013).
- Grenyer, R. *et al.* Global distribution and conservation of rare and threatened vertebrates. *Nature* **444**, 93–96 (2006).
- Pearson, R. G. *et al.* Life history and spatial traits predict extinction risk due to climate change. *Nat. Clim. Chang.* **4**, 217–221 (2014).
- Felton, A. *et al.* Climate change, conservation and management: an assessment of the peer-reviewed scientific journal literature. *Biodivers. Conserv.* **18**, 2243–2253 (2009).
- Dunlop, M. Biodiversity: strategy conservation. *Nat. Clim. Chang.* **3**, 1019–1020 (2013).
- Hoegh-Guldberg, O. *et al.* Assisted colonization and rapid climate change. *Science (80-)*. **321**, 345–346 (2008).
- Thomas, C. D. Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends Ecol. Evol.* **26**, 216–221 (2011).
- Buckley, L. B. & Roughgarden, J. Biodiversity conservation: effects of changes in climate and land use. *Nature* **430**, (2004).
- Harte, J., Ostling, A., Green L., J. & Kinzig, A. Biodiversity conservation: climate change and extinction risk. *Nature* **430**, (2004).
- Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427**, 145–148 (2004).
- Thuiller, W. *et al.* Biodiversity conservation: uncertainty in predictions of extinction risk. *Nature* **430**, (2004).
- Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C. & Mace, G. M. Beyond predictions: biodiversity conservation in a changing climate. *Science (80-)*. **332**, 53–58 (2011).
- Heller, N. E. & Zavaleta, E. S. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Conserv.* **142**, 14–32 (2009).
- Huntley, B. *Climatic change and the conservation of European biodiversity: towards the development of adaptation strategies T-PVS/Inf(2007)03E*. (2007).
- Lawler, J. J. Climate change adaptation strategies for resource management and conservation planning. *Ann. N. Y. Acad. Sci.* **1162**, 79–98 (2009).
- Willis, K. J., Bennett, K. D., Bhagwat, S. A. & Birks, H. J. B. 4 °C and beyond: what did this mean for biodiversity in the past? *Syst. Biodivers.* **8**, 3–9 (2010).
- Gray, S. T. From uncertainty to action: climate change projections and the management of large natural areas. *Bioscience* **61**, 504–505 (2011).
- Coulson, T. *et al.* Age, sex, density, winter weather, and population crashes in Soay sheep. *Science (80-)*. **292**, 1528–1531 (2001).
- Barbraud, C. & Weimerskirch, H. Climate and density shape population dynamics of a marine top predator. *Proc. Biol. Sci.* **270**, 2111–2116 (2003).
- Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81–83 (2006).



39. MacDonald, D. W., Newman, C., Buesching, C. D. & Nouvellet, P. Are badgers “under the weather”? Direct and indirect impacts of climate variation on European badger, (*Meles meles*) population dynamics. *Glob. Chang. Biol.* **16**, 2913–2922 (2010).
40. Gaston, K. J. Geographic range limits: achieving synthesis. *Proc. R. Soc. B Biol. Sci.* **276**, 1395–1406 (2009).
41. Janzen, D. H. Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233–249 (1967).
42. Stevens, G. C. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.* **133**, 240–256 (1989).
43. Milner-Gulland, E. J. & Bennett, E. L. Wild meat: the bigger picture. *Trends Ecol. Evol.* **18**, 351–357 (2003).
44. Roughgarden, J. & Smith, F. Why fisheries collapse and what to do about it. *Proc. Natl. Acad. Sci.* **93**, 5078–5083 (1996).
45. IPCC. *Climate Change 2013 The Physical Science Basis Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (Cambridge University Press, 2013).
46. Suttle, K. B., Thomsen, M. A. & Power, M. E. Species interactions reverse grassland responses to changing climate. *Science (80-. )*. **315**, 640–642 (2007).
47. Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
48. Huntley, B., Collingham, Y. C., Willis, S. G. & Green, R. E. Potential impacts of climatic change on European breeding birds. *PLoS One* **3**, e1439 (2008).
49. Schwartz, M. W. & Martin, T. G. Translocation of imperiled species under changing climates. *Ann. N. Y. Acad. Sci.* **1286**, 15–28 (2013).
50. Possingham, H. P. *et al.* Limits to the use of threatened species lists. *Trends Ecol. Evol.* **17**, 503–507 (2002).
51. Pearson, R. G. & Dawson, T. P. Bioclimate envelope models: what they detect and what they hide — response to Hampe (2004). *Glob. Ecol. Biogeogr.* **13**, 471–473 (2004).
52. Lewis, O. T. Climate change, species-area curves and the extinction crisis. *Phil. Trans. R. Soc. B* **361**, 163–171 (2006).
53. Araújo, M. B., Thuiller, W. & Pearson, R. G. Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* **33**, 1712–1728 (2006).
54. Thuiller, W. *et al.* Consequences of climate change on the tree of life in Europe. *Nature* **470**, 531–534 (2011).
55. Cahill, A. E. *et al.* How does climate change cause extinction? *Proc. R. Soc. B Biol. Sci.* **280**, (2013).
56. Phillimore, A. B., Hadfield, J. D., Jones, O. R. & Smithers, R. J. Differences in spawning date between populations of common frog reveal local adaptation. *Proc. Natl. Acad. Sci.* **107**, 8292–8297 (2010).
57. Hobbs, R. J., Hallett, L. M., Ehrlich, P. R. & Mooney, H. A. Intervention ecology: applying ecological science in the twenty-first century. *Bioscience* **61**, 442–450 (2011).
58. Fuller, R. A. *et al.* Replacing underperforming protected areas achieves better conservation outcomes. *Nature* **466**, 365–367 (2010).
59. Araújo, M. B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. Climate change threatens European conservation areas. *Ecol. Lett.* **14**, 484–492 (2012).
60. McLachlan, J. S., Hellman, J. J. & Schwartz, M. W. A framework for debate of assisted migration in an era of climate change. *Conserv. Biol.* **21**, 297–302 (2007).
61. Botkin, D. B. *et al.* Forecasting the effects of global warming on biodiversity. *Bioscience* **57**, 227–236 (2007).
62. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
63. Root, T. L. *et al.* Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60 (2003).
64. Walther, G.-R. *et al.* Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).
65. Davies, Z. G., Wilson, R. J., Coles, S. & Thomas, C. D. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *J. Anim. Ecol.* **75**, 247–256 (2006).
66. Menéndez, R. *et al.* Species richness changes lag behind climate change. *Proc. R. Soc. B Biol. Sci.* **273**, 1465–1470 (2006).
67. Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B Biol. Sci.* **275**, 2743–2748 (2008).
68. Huntley, B. & Webb III, T. Migration: species’ response to climatic variations caused by changes in the Earth’s orbit. *J. Biogeogr.* **16**, (1989).
69. Jackson, S. T., Betancourt, J. L., Booth, R. K. & Gray, S. T. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proc. Natl. Acad. Sci.* **106**, 19685–19692 (2009).
70. Clark, J. S. *et al.* Reid’s Paradox of Rapid Plant Migration: dispersal theory and interpretation of paleoecological records. *Bioscience* **48**, 13–24 (1998).
71. Cwynar, L. C. & MacDonald, G. M. Geographical variation of Lodgepole Pine in relation to population history. *Am. Nat.* **129**, (1987).
72. Corlett, R. T. & Westcott, D. A. Will plant movements keep up with climate change? *Trends Ecol. Evol.* **28**, 482–488 (2013).
73. MacArthur, R. H. Patterns of species diversity. *Biol. Rev.* **40**, 510–533 (1965).
74. Pearson, R. G. & Dawson, T. P. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biol. Conserv.* **123**, 389–401 (2005).
75. Visser, M. E. Keeping up with a warming world: assessing the rate of adaptation to climate change. *Proc. R. Soc. B Biol. Sci.* **275**, 649–659 (2008).
76. Rowe, K. C., Heske, E. J., Brown, P. W. & Paige, K. N. Surviving the ice: Northern refugia and postglacial colonization. *Proc. Natl. Acad. Sci. U. S. A.* **101**, 10355–10359 (2004).
77. McLachlan, J. S., Clark, J. S. & Manos, P. S. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* **86**, 2088–2098 (2005).
78. Premoli, A. C., Kitzberger, T. & Veblen, T. T. Isozyme variation and recent biogeographical history of the long-lived conifer *Fitzroya cupressoides*. *J. Biogeogr.* **27**, 251–260 (2000).
79. Chevin, L.-M., Lande, R. & Mace, G. M. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* **8**, e1000357 (2010).

## About the authors

**Dr Maria Dickinson** is a research associate at the Grantham Institute at Imperial College London. She focusses on examining methods and frameworks for increasing understanding and improving predictions of the potential impacts of climate change and other anthropogenic threats on species and ecosystems. Her work involves broad-scale biogeographical approaches, including generation of global metrics to allow identification of species or regions of greatest sensitivity, exposure and vulnerability to climate change. She also applies population modelling approaches to explore the potential effect of differences between species biological traits on their sensitivity and adaptability to climate change.

**Professor Iain Colin Prentice** has a background in palaeoecology and has carried out research in ecological data analysis, vegetation dynamics and biogeochemical modelling, biosphere-atmosphere interactions and the global carbon cycle. He was a pioneer of global vegetation modelling and led the development of the widely used BIOME and LPJ families of models. He has held professorships at Lund, Bristol and Macquarie Universities, was a founding Director of the Max Planck Institute for Biogeochemistry, and led the UK's flagship QUEST research programme on Earth System Science. He now holds the AXA Chair of Biosphere and Climate Impacts at Imperial College London. His current research aims to discover fundamental principles governing the adaptive responses of plant and ecosystem processes to environmental variations, and to apply these in a new generation of global models to assess the potential impacts of climate change on the natural world.

**Professor Georgina M. Mace** is Professor of Biodiversity and Ecosystems, and Head of the Centre for Biodiversity and Environment Research at University College London. Her research concerns measuring the trends and consequences of biodiversity loss and change with a particular focus on the science and policy interface for biodiversity conservation and ecosystem management. She worked on the biodiversity elements of the Millennium Ecosystem Assessment and contributed to the technical development of measures for the CBD 2010 biodiversity target. She worked on the UK National Ecosystem Assessment (2011) and the IPCC WG2 report (2014). In 2014 she chaired a Royal Society science policy report on "Resilience to extreme weather". Currently she is a member of the UK Government's Natural Capital Committee (2012-2015).

80. Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merilä, J. Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* **17**, 167–178 (2008).
81. Vedder, O., Bouwhuis, S. & Sheldon, B. C. Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS Biol* **11**, e1001605 (2013).
82. Valladares, F. *et al.* The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecol. Lett.* **17**, 1351–1364 (2014).
83. Fitter, A. H. & Fitter, R. S. R. Rapid changes in flowering time in British plants. *Science (80- )*. **296**, 1689–1691 (2002).
84. Beebee, T. J. C. Amphibian breeding and climate. *Nature* **374**, 219–220 (1995).
85. Both, C., Bijlsma, R. G. & Visser, M. E. Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. *J. Avian Biol.* **36**, 368–373 (2005).
86. Bradshaw, W. E. & Holzapfel, C. M. Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci.* **98**, 14509–14511 (2001).
87. Williams, J. W. & Jackson, S. T. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5**, 475–482 (2007).
88. Bennie, J., Kubin, E., Wiltshire, A., Huntley, B. & Baxter, R. Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: the implications of local adaptation to climate. *Glob. Chang. Biol.* **16**, 1503–1514 (2010).
89. Both, C. & Visser E., M. The effect of climate change on the correlation between avian life history traits. *Glob. Chang. Biol.* **11**, 1606–1613 (2005).
90. Oswald, S. A., Bearhop, S., Furness, R. W., Huntley, B. & Hamer, K. C. Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas *Catharacta skua*. *J. Avian Biol.* **39**, 163–169 (2008).
91. Bradshaw, A. D. & McNeilly, T. Evolutionary response to global climatic change. *Ann. Bot.* **67**, 5–14 (1991).
92. 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.* **104**, 1278–1282 (2007).
93. Huntley, B. Evolutionary response to climatic change. *Heredity (Edinb.)* **98**, 247–248 (2007).
94. Plard, F. *et al.* Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biol* **12**, e1001828 (2014).
95. Pounds, J. A. *et al.* Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167 (2006).
96. Foden, W. *et al.* A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Divers. Distrib.* **13**, 645–653 (2007).
97. Ockendon, N. *et al.* Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Glob. Chang. Biol.* **20**, 2221–2229 (2014).
98. Warren, M. S. *et al.* Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69 (2001).

99. Cunningham, S. J., Martin, R. O., Hojem, C. L. & Hockey, P. A. R. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of common fiscals. *PLoS One* **8**, e74613 (2013).
100. Parmesan, C., Duarte, C., Poloczanska, E., Richardson, A. J. & Singer, M. C. Overstretching attribution. *Nat. Clim. Chang.* **1**, 2–4 (2011).
101. Jackson, S. T. & Sax, D. F. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* **25**, 153–160 (2010).
102. Campos, P. F. *et al.* Ancient DNA sequences point to a large loss of mitochondrial genetic diversity in the saiga antelope (*Saiga tatarica*) since the Pleistocene. *Mol. Ecol.* **19**, 4863–4875 (2010).
103. Campos, P. F. *et al.* Ancient DNA analyses exclude humans as the driving force behind late Pleistocene musk ox (*Ovibos moschatus*) population dynamics. *Proc. Natl. Acad. Sci.* **107**, 5675–5680 (2010).
104. Blois, J. L., McGuire, J. L. & Hadly, E. A. Small mammal diversity loss in response to late-Pleistocene climatic change. *Nature* **465**, 771–774 (2010).
105. Jackson, S. T. & Overpeck, J. T. Responses of plant populations and communities to environmental changes of the Late Quaternary. *Paleobiology* **26**, 194–220 (2000).
106. Koch, P. L. & Barnosky, A. D. Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Syst.* **37**, 215–250 (2006).
107. Isaac, N. J. B. & Cowlshaw, G. How species respond to multiple extinction threats. *Proc. R. Soc. B Biol. Sci.* **271**, 1135–1141 (2004).
108. Purvis, A., Cardillo, M., Grenyer, R. & Collen, B. Correlates of extinction risk: phylogeny, biology, threat and scale, in *Phylogeny and Conservation*. (Purvis, A., Brooks, T. M. & Gittleman, J. L.) Eds 295–316 (Cambridge: Cambridge University Press, 2005).
109. Araújo, M. B., Cabeza, M., Thuiller, W., Hannah, L. & Williams, P. H. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Glob. Chang. Biol.* **10**, 1618–1626 (2004).
110. Hole, D. G. *et al.* Projected impacts of climate change on a continent-wide protected area network. *Ecol. Lett.* **12**, 420–431 (2009).
111. Dormann, C. F. Promising the future? Global change projections of species distributions. *Basic Appl. Ecol.* **8**, 387–397 (2007).
112. Schurr, F. M. *et al.* How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *J. Biogeogr.* **39**, 2146–2162 (2012).
113. Soberón, J. & Nakamura, M. Niches and distributional areas: concepts, methods and assumptions. *Proc. Natl. Acad. Sci.* **106**, 19644–19650 (2009).
114. Williams, J. W., Jackson, S. T. & Kutzbach, J. E. Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci.* **104**, 5738–5742 (2007).
115. Randin, C. F. *et al.* Climate change and plant distribution: local models predict high-elevation persistence. *Glob. Chang. Biol.* **15**, 1557–1569 (2009).
116. Díaz, S. *et al.* Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.* **3**, 2958–2975 (2013).
117. Lawler, J. J. *et al.* Projected climate-induced faunal change in the Western Hemisphere. *Ecology* **90**, 588–597 (2009).
118. Hobbs, R. J., Higgs, E. & Harris, J. A. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* **24**, 599–605 (2009).
119. Murcia, C. *et al.* A critique of the “novel ecosystem” concept. *Trends Ecol. Evol.* **29**, 548–553 (2014).
120. Sanderson, E. W. *et al.* The Human Footprint and the Last of the Wild. *Bioscience* **52**, 891–904 (2002).
121. Durant, S. Non-native species: UK bill could prompt biodiversity loss. *Nature* **512**, 253 (2014).
122. Hayward, M. W. Conservation management for the past, present and future. *Biodivers. Conserv.* **18**, 765–775 (2009).
123. Lawton, J. H. *et al.* *Making Space for Nature: a review of England's wildlife sites and ecological network. Report to Defra.* (2010).
124. Peterson, G. D., Cumming, G. S. & Carpenter, S. R. Scenario planning: a tool for conservation in an uncertain world. *Conserv. Biol.* **17**, 358–366 (2003).

## About the Grantham Institute

The Grantham Institute is committed to driving research on climate change and the environment, and translating it into real world impact. Established in February 2007 with a £12.8 million donation over ten years from the Grantham Foundation for the Protection of the Environment, the Institute's researchers are developing both the fundamental scientific understanding of climate and environmental change, and the mitigation and adaptation responses to it. The research, policy and outreach work that the Institute carries out is based on, and backed up by, the world-leading research by academic staff at Imperial.

[www.imperial.ac.uk/grantham](http://www.imperial.ac.uk/grantham)

## About Imperial College London

Consistently rated amongst the world's best universities, Imperial College London is a science-based institution with a reputation for excellence in teaching and research that attracts 13,000 students and 6,000 staff of the highest international quality.

Innovative research at the College explores the interface between science, medicine, engineering and business, delivering practical solutions that improve quality of life and the environment—underpinned by a dynamic enterprise culture. Since its foundation in 1907, Imperial's contributions to society have included the discovery of penicillin, the development of holography and the foundations of fibre optics.

This commitment to the application of research for the benefit of all continues today, with current focuses including interdisciplinary collaborations to improve health in the UK and globally, tackle climate change and develop clean and sustainable sources of energy.

[www.imperial.ac.uk](http://www.imperial.ac.uk)

125. Huntley, B. *An analysis of the implementation of recommendations made by the group of experts on biodiversity and climate change (2006-2011)*. *T-PVS/Inf* (2012) 11. (2012).
126. Beale, C. M., Baker, N. E., Brewer, M. J. & Lennon, J. J. Protected area networks and savannah bird biodiversity in the face of climate change and land degradation. *Ecol. Lett.* **16**, 1061–1068 (2013).
127. Johnston, A. *et al.* Observed and predicted effects of climate change on species abundance in protected areas. *Nat. Clim. Chang.* **3**, 1055–1061 (2013).
128. Thomas, C. D. *et al.* Protected areas facilitate species' range expansions. *Proc. Natl. Acad. Sci.* **109**, 14063–14068 (2012).
129. Mace, G. M., Gittleman, J. L. & Purvis, A. Preserving the Tree of Life. *Science*. **300**, 1707–1709 (2003).
130. Hole, D. G. *et al.* Toward a management framework for networks of protected areas in the face of climate change. *Conserv. Biol.* **25**, 305–315 (2011).
131. Williams, P. *et al.* Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conserv. Biol.* **19**, 1063–1074 (2005).
132. Hannah, L. Protected area needs in a changing climate. *Front. Ecol. Environ.* **5**, 131 (2007).
133. Anderson, M. G. & Ferree, C. E. Conserving the stage: climate change and the geophysical underpinnings of species diversity. *PLoS One* **5**, e11554 (2010).
134. Hunter, M. L., Jacobson, G. L. & Webb, T. Paleocology and the coarse-filter approach to maintaining biological diversity. *Conserv. Biol.* **2**, 375–385 (1988).
135. Pyke, C. R. & Fischer, D. T. Selection of bioclimatically representative biological reserve systems under climate change. *Biol. Conserv.* **121**, 429–441 (2005).
136. Ricciardi, A. & Simberloff, D. Assisted colonization is not a viable conservation strategy. *Trends Ecol. Evol.* **24**, 248–253 (2009).
137. Marris, E. Moving on assisted migration. *Nat. Reports Clim. Chang.* 112–113 (2008). at <http://dx.doi.org/10.1038/climate.2008.86>
138. Parmesan, C. Climate and species' range. *Nature* **382**, 765–766 (1996).
139. Hedrick, P. W. Gene flow and genetic restoration: the Florida panther as a case study. *Conserv. Biol.* **9**, 996–1007 (1995).
140. Johnson, W. E. *et al.* Genetic restoration of the Florida panther. *Science (80-)*. **329**, 1641–1645 (2010).
141. Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A. & Loeuille, N. Eco-evolutionary responses of biodiversity to climate change. *Nat. Clim. Chang.* **2**, 747–751 (2012).
142. Urban, M. C., Tewksbury, J. J. & Sheldon, K. S. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proc. R. Soc. B Biol. Sci.* **279**, 2072–2080 (2012).
143. Kirkpatrick, M. & Barton, N. A. H. Evolution of a species' range. *Am. Nat.* **150**, 1–23 (1997).
144. Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. Putting the heat on tropical animals. *Science (80-)*. **320**, 1296–1297 (2008).
145. UN-REDD Programme. UN-REDD Programme. <http://www.un-redd.org/>
146. Balmford, A. & Whitten, T. Who should pay for tropical conservation, and how could the costs be met? *Oryx* **37**, 238–250 (2003).
147. James, A. N., Gaston, K. J. & Balmford, A. Balancing the Earth's accounts. *Nature* **401**, 323–324 (1999).
148. Ozgul, A. *et al.* Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**, 482–485 (2010).
149. Keith, D. A. *et al.* Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* **4**, 560–563 (2008).
150. Doak, D. F. *et al.* Understanding and predicting ecological dynamics: are major surprises inevitable. *Ecology* **89**, 952–961 (2008).
151. Early, R. & Sax, D. F. Analysis of climate paths reveals potential limitations on species range shifts. *Ecol. Lett.* **14**, 1125–1133 (2011).
152. Gaston, K. J. Global patterns in biodiversity. *Nature* **405**, 220–227 (2000).
153. Conservation International. Hotspots. <http://www.conservation.org/How/Pages/Hotspots.asp>
154. Mora, C. *et al.* The projected timing of climate departure from recent variability. *Nature* **502**, 183–187 (2013).
155. Loss, S. R., Terwilliger, L. A. & Peterson, A. C. Assisted colonization: integrating conservation strategies in the face of climate change. *Biol. Conserv.* **144**, 92–100 (2011).
156. Marcott, S. A., Shakun, J. D., Clark, P. U. & Mix, A. C. A reconstruction of regional and global temperature for the past 11,300 years. *Science (80-)*. **339**, 1198–1201 (2013).
157. Lambert, F. *et al.* Dust-climate couplings over the past 800,000 years from the EPICA Dome C ice core. *Nature* **452**, 616–619 (2008).
158. Harrison, S. P. & Sanchez Goñi, M. F. Global patterns of vegetation response to millennial-scale variability and rapid climate change during the last glacial period. *Quat. Sci. Rev.* **29**, 2957–2980 (2010).
159. Birks, H. H. & Ammann, B. Two terrestrial records of rapid climatic change during the glacial–Holocene transition (14,000–9,000 calendar years B.P.) from Europe. *Proc. Natl. Acad. Sci.* **97**, 1390–1394 (2000).
160. Steffensen, J. P. *et al.* High-resolution Greenland ice core data show abrupt climate change happens in few years. *Science (80-)*. **321**, 680–684 (2008).
161. Harrison, S. P. & Prentice, I. C. Climate and CO<sub>2</sub> controls on global vegetation distribution at the last glacial maximum: analysis based on palaeovegetation data, biome modelling and palaeoclimate simulations. *Glob. Chang. Biol.* **9**, 983–1004 (2003).
162. Keenan, T., Josep, M. S., Lloret, F., Ninyerola, M. & Sabate, S. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO<sub>2</sub> matters! *Glob. Chang. Biol.* **17**, 565–579 (2011).

