



Multiple Dimensions of Climate Change and Their Implications for Biodiversity

Raquel A. Garcia *et al.*
Science **344**, (2014);
DOI: 10.1126/science.1247579

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of May 21, 2014):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/344/6183/1247579.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2014/04/30/344.6183.1247579.DC1.html>

This article **cites 135 articles**, 25 of which can be accessed free:

<http://www.sciencemag.org/content/344/6183/1247579.full.html#ref-list-1>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>

S READ THE FULL ARTICLE ONLINE
<http://dx.doi.org/10.1126/science.1247579>

A framework is proposed to guide the selection and integration of different climate-change metrics in biodiversity impact assessments.

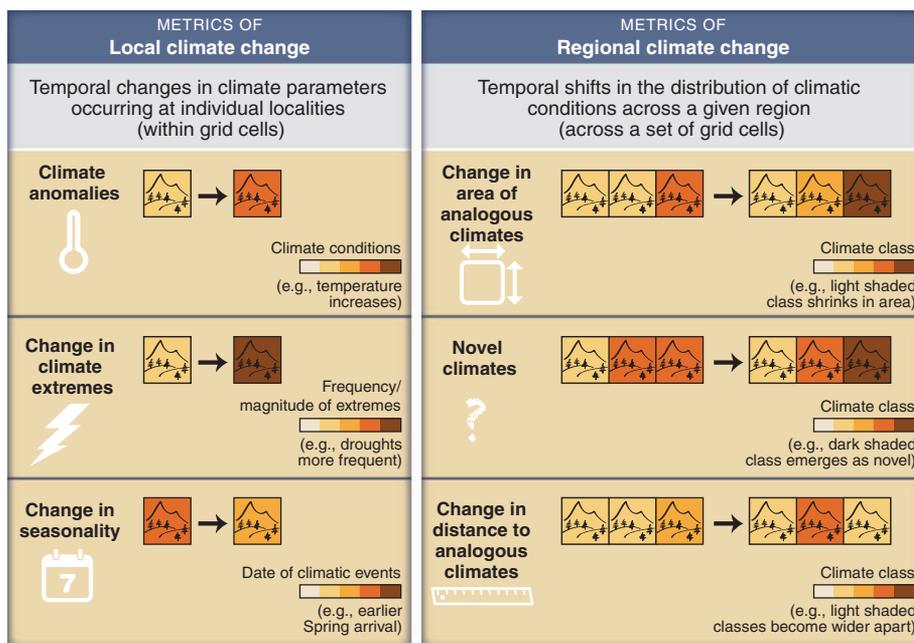
Multiple Dimensions of Climate Change and Their Implications for Biodiversity

Raquel A. Garcia,* Mar Cabeza, Carsten Rahbek, Miguel B. Araújo*

Background: Changes in Earth's climate over time can be measured in many ways. The different metrics available represent alternative dimensions of climate change, each with distinct implications for biodiversity conservation and other sectors. However, this diversity is rarely recognized. At any given locality, average temperature or precipitation can increase or decrease, extreme values can become more intense or frequent, and the timing of specific climatic events can shift. At the same time, climatic conditions are redistributed at broader spatial extents. Across sets of localities, particular climatic conditions can become more or less available and can shift closer or farther in position at different velocities. Metrics quantifying these and other dimensions of change are commonly used in basic and applied sciences. In ecological contexts, individual metrics have helped to explain the role of past climate changes in driving species diversity or extinctions and to forecast the exposure of biodiversity to future climate changes. Yet, a comparison of the many alternative metrics in use is lacking to gain understanding of their properties and guide their use in biodiversity assessments.

Advances: Our review demonstrates that six commonly used metrics of climate change show contrasting patterns under 21st-century climate forecasts across the world. For example, whereas polar climates are projected to warm and shrink in area, the tropics see the emergence of novel climatic conditions and undergo local changes in average climates beyond past variability. To help interpret metrics of climate change, our review critically assesses the ecological implications of different metrics. Supported by examples of empirical links between observed changes in biological systems and different dimensions of climate change, we outline a conceptual framework for classification of climate change metrics according to the types of threat and opportunity they are likely to impose on biodiversity. Climate changes at the locality level are often associated with demographic threats and opportunities at the population level, whereas changes across localities can have positive or negative implications for the size and the position of species' ranges.

Outlook: Forecasting the long-term impacts of future climate changes on biodiversity is challenging, not least because the responses of organisms are contingent on demographic, physiological, and evolutionary mechanisms, as well as on the interaction with other human-induced stressors such as habitat fragmentation. Lack of data for the majority of species on Earth further hampers the use of available bioclimatic modeling methods. By contrast, the use of simple metrics of climate change is more easily scalable to wholesale biodiversity. When appropriately implemented, such examination can provide a first-order assessment of the challenges that species are potentially exposed to, and in many circumstances, it might be the only option available.



The diversity of metrics of climate change. Climate parameters, such as temperature or precipitation, can change at individual localities over time (left), whereas shifts in the distribution of climatic conditions across sets of localities can also occur (right). Local metrics can quantify changes in the magnitude of average or extreme values, as well as shifts in the timing of climatic events. Regional metrics describe how specific climatic conditions may increase or decrease in area, become more dissimilar to past climatic conditions, or move in space. These and other commonly used metrics of climate change describe different dimensions of change and are expected to relate to distinct challenges for biodiversity. Different metrics thus provide complementary information when describing future climates and their potential effects. Examining metrics in combination can show how they interact to exacerbate or lessen species' exposure to climate change.

The list of author affiliations is available in the full article online.

*Corresponding author. E-mail: raquel.ag@gmail.com (R.A.G.); miguel.araujo@imperial.ac.uk (M.B.A.)

Cite this article as R. A. Garcia *et al.*, *Science* **344**, 1247579 (2014). DOI: 10.1126/science.1247579

Multiple Dimensions of Climate Change and Their Implications for Biodiversity

Raquel A. Garcia,^{1,2,3,4*} Mar Cabeza,⁴ Carsten Rahbek,^{2,5} Miguel B. Araújo^{1,2,3,5*}

The 21st century is projected to witness unprecedented climatic changes, with greater warming often reported for high latitudes. Yet, climate change can be measured in a variety of ways, reflecting distinct dimensions of change with unequal spatial patterns across the world. Polar climates are projected to not only warm, but also to shrink in area. By contrast, today's hot and arid climates are expected to expand worldwide and to reach climate states with no current analog. Although rarely appreciated in combination, these multiple dimensions of change convey complementary information. We review existing climate change metrics and discuss how they relate to threats and opportunities for biodiversity. Interpreting climate change metrics is particularly useful for unknown or poorly described species, which represent most of Earth's biodiversity.

The interaction between the climatic changes projected for the 21st century and other ongoing human-induced threats, such as habitat loss, presents a major challenge to biodiversity (1, 2). Accurate forecasts of climate change effects on biodiversity are thus required to address broader societal commitments toward natural resource management and conservation (3, 4). To address this problem, researchers have developed a range of bioclimatic models. Statistical models (5) measure species' exposure to climate change by relating species' distributions to aspects of climate. By contrast, mechanistic models explicitly consider demographic (6) and physiological (7) processes to predict species' responses to climate change exposure. Given the limited availability of demographic and physiological data, most assessments of climate change effects on biodiversity use statistical rather than process-based models. Yet, for most species on Earth, distributional data are also lacking so that even the simplest statistical model cannot be fitted. An alternative is to use simple metrics of climate change to quantify the exposure of areas to different dimensions of change and relate these dimensions to different threats and opportunities for biodiversity [e.g., (8–11)].

The anomalies in climate parameters at any given locality over time are a commonly used

metric, but a vast array of alternative metrics exists. They include temporal differences in extreme events, such as droughts; decreases or increases in total area with given climatic conditions; and the velocity at which climate moves across space and time. Such climate change metrics have been applied to a variety of questions. For example, when coupled with climate hindcasts, they have been used to examine the role of historical climatic changes in species richness gradients (12–15), the geographical distribution of centers of diversity (16) or past climatic refugia (17, 18), the pace of distributional shifts of species over past decades (19) or millennia (20), the risk of species extinctions (21), and the degree of biotic network specialization across latitude (22). When coupled with climate change forecasts, they have supported risk assessments for biodiversity (8, 10, 11, 23–27) and conservation areas (9, 28–30), while also enabling the identification of potential regional pools of species (31).

Despite the increased use of climate change metrics in basic and applied sciences, the variety of existing metrics and their ecological implications have hitherto not been fully appreciated. Studies spanning different geographical areas have used single metrics (11, 16, 26, 29) more frequently than multiple metrics in combination (21, 23, 24). A comprehensive comparison of metrics, including the analysis of their global patterns and implications for biodiversity, is thus needed to gain understanding of their properties and guide their use. Here, we review the climate change metrics commonly used in biodiversity assessments. We first describe the different types of metrics and illustrate their differences by implementing six of the most commonly used metrics with global 21st-century climate projections. We then explore how the different metrics capture distinct dimensions of climate change and carry complementary information that is vital for understanding the potential im-

pacts of ongoing climate changes on biodiversity. Finally, we outline a conceptual framework for linking the different metrics to assessments of threat and opportunity for species and discuss its advantages and limitations.

Climate Change Metrics

Metrics of climate change describe temporal changes in single or multiple climate parameters, such as temperature or precipitation. Existing metrics fall into one of two categories (Box 1 and table S1). They measure either temporal changes in climate parameters at individual localities (hereafter termed “local metrics”), or shifts in the distribution of climatic conditions over space and time (hereafter termed “regional metrics”). Beyond the geographical context of the measurements, metrics can also characterize different dimensions of climate change. For example, local metrics can characterize the magnitude of changes by quantifying how average (23, 32) or extreme (10, 26) values of climate are altered in a given locality (cell) over time. Shifts in the timing of climatic events can also be measured at the locality level (13, 33). In turn, regional metrics begin with the characterization of climatic conditions across a given region and then measure temporal changes in the availability of analogous climatic conditions across that region (23, 34, 35), as well as changes in the direction to, or distance between, the positions of analogous climatic conditions (34). Within the region neighboring any given locality, the velocity at which climate shifts its position can also be quantified (9, 16).

Mapping Multiple Dimensions of Climate Change

Although several metrics of climate change exist, they have typically been applied in isolation. Implementation of six common climate change metrics worldwide reveals that each characterizes different, sometimes opposing, patterns (Fig. 1). Local climate anomalies are projected to affect the tropics, subtropics, and northern high latitudes. More than half the global area currently covered by tropical climates faces large changes in average climate in relation to historical interannual variability (Fig. 2; for more details, see fig. S3). Large anomalies are also projected for more than 30% of the area of polar climates. The extreme drying and warming events explored here are projected to affect mainly the tropics. However, changes in other local extreme events may produce different patterns, with metrics describing extreme seasonal or annual precipitation and extreme daily maximum temperatures, for example, highlighting the high latitudes (36, 37).

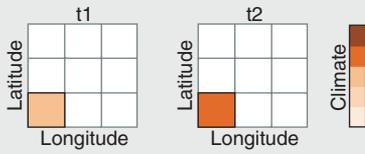
In turn, regional metrics describing changes in the area covered by different climate types reveal a trend toward expansion of the hot arid climates of the Sahara, southern Africa, and Australia, accompanied by reductions in the area of polar and mountain climates. The climatic

¹Department of Biogeography and Global Change, National Museum of Natural Sciences, Consejo Superior de Investigaciones Científicas, Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain.

²Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark. ³Research Network in Biodiversity and Evolutionary Biology (InBio)—Research Center in Biodiversity and Genetic Resources (CIBIO), University of Évora, Largo dos Colegiais, 7000 Évora, Portugal. ⁴Metapopulation Research Group, Department of Biosciences, University of Helsinki, FIN-00014 Helsinki, Finland. ⁵Imperial College London, Silwood Park, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK.

*Corresponding author. E-mail: raquel.ag@gmail.com (R.A.G.); miguel.araujo@imperial.ac.uk (M.B.A.)

Local change



Box 1: Metrics of climate change.

Panel 1. Metrics of climate change within a grid cell. From period *t1* to *t2*, the climate within a given cell (lower left corner) is altered on a scale that can represent average or extreme climates, or the timing of climatic events.

Examples of metrics

MAGNITUDE

Examples of ecological applications

Anomalies: the difference in climate parameters at a given locality over time.

Examining the influence of Quaternary climate changes on European dung beetle (14) and amphibian and reptile (12) diversity patterns, and of future climate changes across global mountain systems (116).

*Standardized anomalies**: the Euclidean distance between baseline and future climate at a given locality, standardized by historical interannual climate variability (23).

Examining the exposure of different localities (cells) worldwide to future climate changes in relation to existing biodiversity (23, 24).

*Change in the probability of extremes**: the difference over time, at a given locality, in the magnitude of extreme climatic events, or in the probability of occurrence of the most extreme historical climatic event (117).

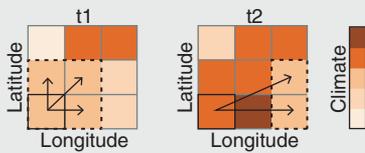
Examining the influence of extreme climates on invasion susceptibility of plant communities in north-central Chile over the past decades (26).

TIMING

Change in seasonality: the difference over time in the timing of climatic events.

Assessing the role of delayed snowmelt on the hibernation emergence date of ground squirrels in Canada (33).

Regional change



Panel 2. Metrics of change across grid cells. Between periods *t1* and *t2*, the climate of a given cell (lower left corner) becomes less available across the entire region (from four to two cells), and more distant (longer arrows). The lightest shade in *t1* corresponds to disappearing climates, whereas the darkest shade in *t2* emerges as a novel climate.

Examples of metrics

AVAILABILITY

Examples of ecological applications

*Change in area of analogous climates**: the change over time in area experiencing similar climates [defined with reference to the difference between climates (23, 34), classification rules (118), histograms (35), or clustering analysis (119)].

Exploring climate determinants of centers of rarity for Northern Hemisphere plant, bird, and butterfly species (8), and assessing the role of changes in Late Quaternary climate availability on mammal extinctions (21).

*Novel climates**: emergence of future climatic conditions not found at present [future conditions that are most dissimilar to baseline climates (23), that do not overlap with present conditions in environmental space (29), or that lack baseline-analogs as defined above]. Conversely, disappearing climates refer to the disappearance of extant climates.

Examining plant associations in eastern North America over the past 18,000 years, and testing whether the associations most dissimilar to today's associations occur in areas where past climates were also most dissimilar to today's climates (76, 77).

POSITION

*Change in distance to analogous climates**: the change over time in the distance to similar climates (as defined above for the change in area of analogous climates).

Assessing the role of Late Quaternary climate movements on mammal extinctions (21).

*Climate change velocity**: the ratio of the temporal climatic gradient at a given locality to the spatial climatic gradient across neighboring cells (9).

Predicting climate residence time in global protected areas (9), and comparing past climate velocities to Australian bird distribution shifts (19) and to global vertebrate endemism (16).

*Climate change metric implemented in our global comparison of climate change patterns.

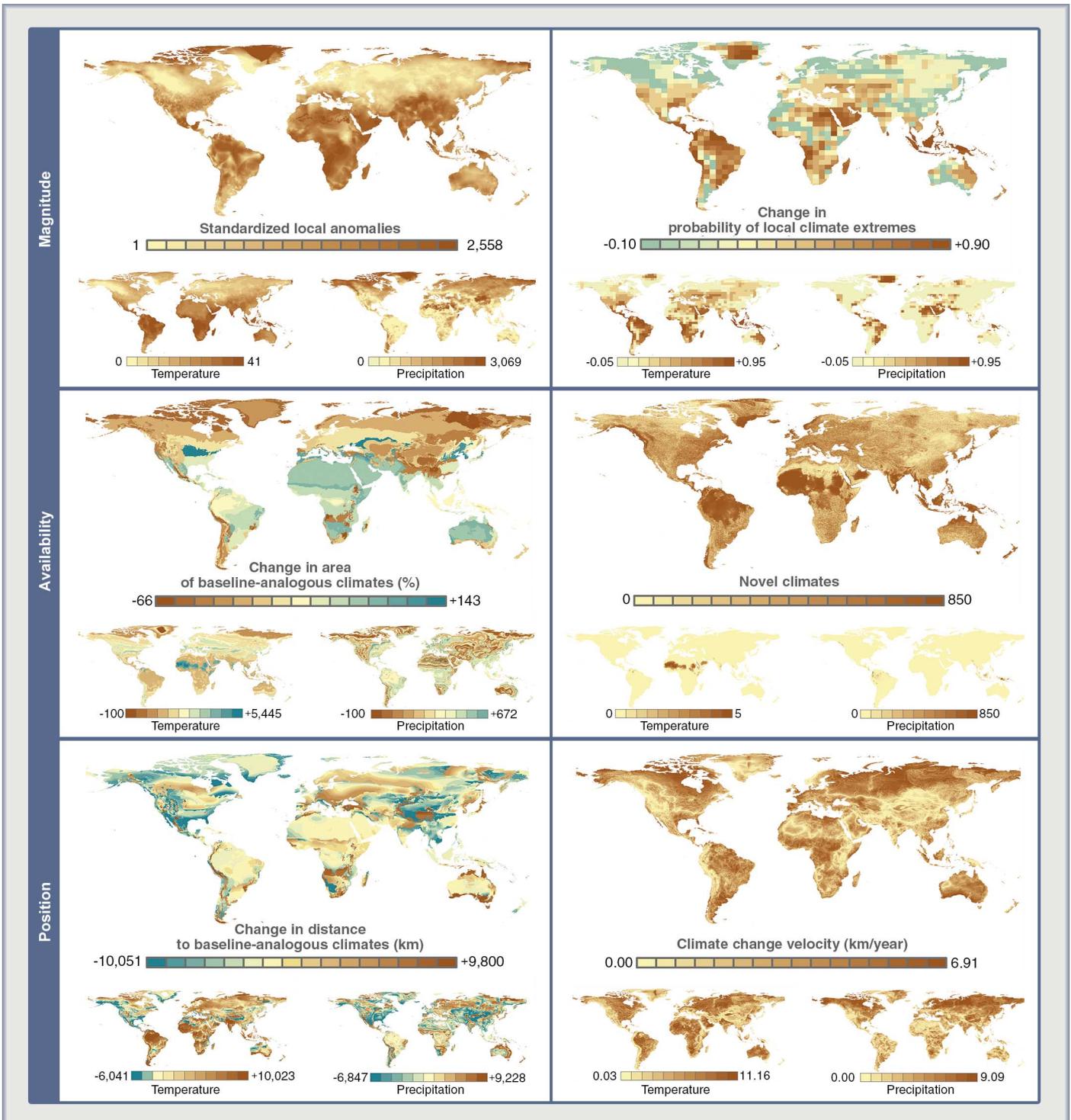


Fig. 1. Projected global climate change according to six metrics. The maps show projections of change in mean annual temperature and total annual precipitation between the baseline and an end-of-century multimodel ensemble under the A1B emissions scenario (120). The metrics illustrated characterize three dimensions of climate change: the magnitude of local changes in average or extreme climates [standardized climate anomalies (23) and change in the probability of extreme climates (117)], changes in the regional availability of climatic conditions [change in area of analogous climates (34, 118), and novel climates (23)], and regional shifts in the position of climatic conditions [change in distance to analogous climates (34, 118), and climate change velocity (9, 16)]. Among the several methodologies available

to compute these metrics (table S1), we selected methodologies that are commonly used. Pairwise spatial correlation between these metrics was significant but generally low (table S2). In each panel, the main maps show changes for temperature and precipitation combined, and the smaller maps show changes for each climate parameter individually. The scales were defined using quantiles and reflect a gradient from small changes (light brown shades) to large changes (dark brown shades), or from favorable changes (blue shades) to adverse changes (brown shades). Local anomalies, novel climates, and climate change velocity values were converted to logarithmic scale for visualization. See figs. S1 and S2 for analysis of sensitivity to alternative climate models.

conditions over the polar region and major mountains across the world are projected to shrink by up to 66%. By contrast, novel climates are more likely to emerge in the tropics and subtropics, owing to warmer temperatures: End-of-century temperatures for 62% of the world's tropical areas are projected to be the most dissimilar from today's temperatures. In about a third of the temperate and polar regions, distances to similar climatic conditions will increase more than anywhere else on the globe. The velocity of changes in temperature and precipitation is forecast to be high in such latitudes, but also in the tropical regions of central Africa, the western Amazon, and southern Australia.

Examining metrics in combination shows that different areas are exposed to different dimensions of climate change. The global patterns are far more complex than the often reported disproportionate warming for land areas at higher northern latitudes (38). In the polar regions, reductions in the global availability of similar climatic conditions are by far the greatest threat among all three dimensions examined (Fig. 2). The tropics and, to a lesser extent, hot arid regions are exposed to the emergence of climatic conditions lacking current analogs, and to changes of great magnitude in average climates and in extreme drying and warming events. Temperate regions are exposed almost equally to all dimensions of change, whereas cold regions are particularly exposed to large-distance or high-velocity shifts in the position of prevailing climates.

Linking Metrics to Threats and Opportunities for Biodiversity

Our global implementation of metrics shows that different climate change metrics have different spatial patterns around the world, but the question remains as to what the implications of each are for biodiversity. We outline a conceptual framework that describes the links between metrics of climate change and the potential extrinsic threats and opportunities that such changes represent for biodiversity (Fig. 3). The framework assumes that suitable climates for species exist where species presently occur, and it is based on two principles. First, under changing climates, and all else being equal, persistence of local populations is more likely where climatic conditions remain suitable (39, 40). Second, the survival of species requires, among other factors, the continued availability of suitable climatic conditions either within or outside the present ranges of species (41). Under these general principles, local changes can be seen as a proxy for demographic threats and opportunities acting at the population level, whereas regional changes in climate can have negative or positive implications for the size and position of entire species' ranges. Support for the suggested links between climate change metrics and threats or opportunities for biodiversity (Fig. 3) can be found in studies cov-

ering a variety of taxonomic groups across regions.

Threats and Opportunities from Local Climate Change

All else being equal, large changes in climate at the local (cell) level are more likely to result in large changes in local suitability for populations than small changes, particularly when climate changes exceed past local variability (23). Decreased local climatic suitability can have effects on the physiology, morphology, or behavior of the organisms in a population (42), potentially leading to changes in population dynamics. Two examples are the reported local extinctions of lizards

in Mexico, attributed to reduced activity of individuals during warmer reproductive seasons (43), and the mortality and population declines at the retracting margin of *Aloe* trees in the Namib desert, owing to desiccation stress (44). Nested within gradual trends (45), changes in extreme climates may pose even greater threats to populations (46). For instance, increased tree mortality across the globe over the last decades has been attributed to drought- and heat-induced stress (47). Positive changes in local suitability for populations under warming or altered rainfall patterns are less frequently documented, but include reports of higher fitness in common lizards in southern France resulting from an increase in body size (48),

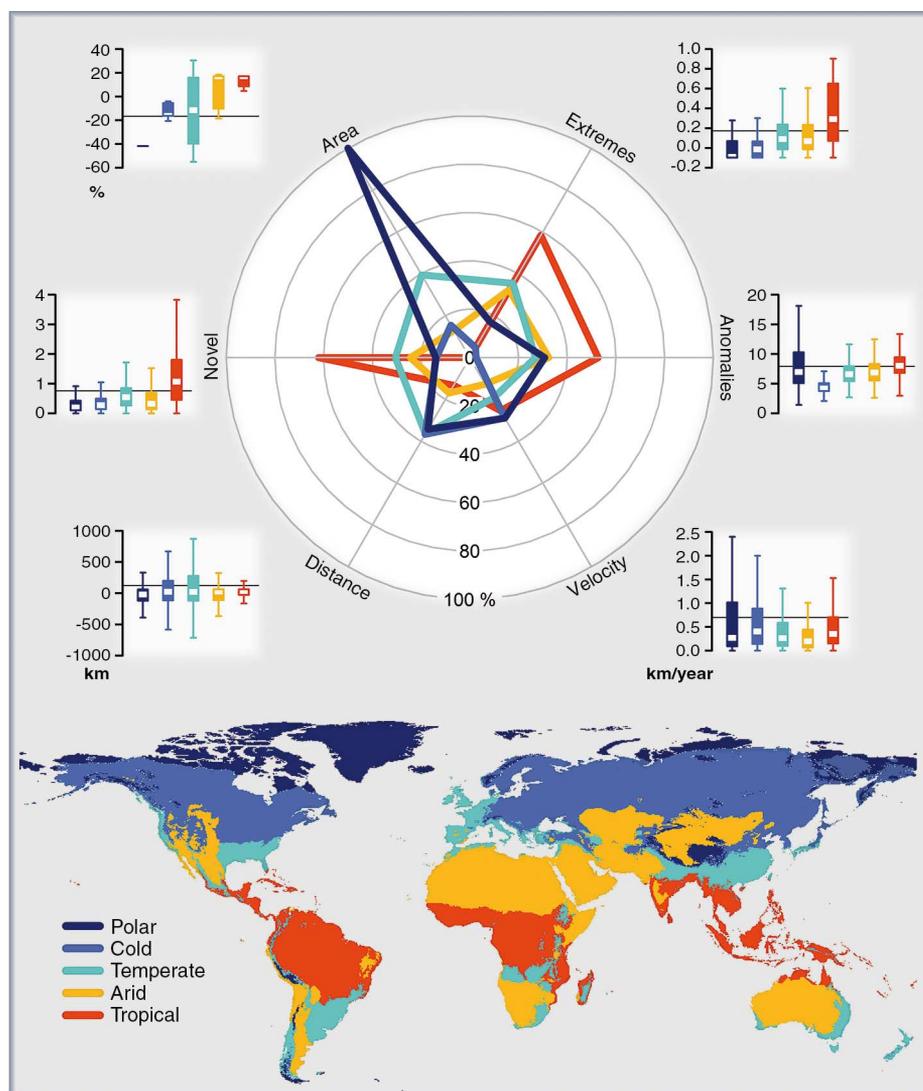


Fig. 2. Exposure of the world's climatic regions to different climate change dimensions. The star plot (upper panel) shows the percentage of area of different climatic regions of the world that are exposed to large changes in six climate change metrics (values above the 75th percentile of the worldwide distribution of values) capturing the magnitude of local changes in average or extreme climates, and regional changes in the availability and position of climatic conditions (120). For each metric, the distribution of values across climatic regions is shown in boxplots, with the horizontal lines indicating the 75th percentile. The colors on the star plot and boxplots correspond to the Köppen-Geiger broad climatic regions represented on the map (bottom panel; see fig. S4). See fig. S5 for analysis of sensitivity to alternative climate models.

increased growth and population numbers of plants in high-latitude ecosystems (49, 50), and increased abundance of Svalbard reindeer during phases of population growth (51).

In turn, shifts in the timing of climatic events can lead to populations altering the timing of seasonal activities such as migration, flowering, or breeding, with potential consequences for the demography and population dynamics of species and communities (52, 53). Such phenological shifts are commonly observed in response to

climate change (54) and have been linked to the seasonality of climate (33), but also to trends in climatic averages (55) and extremes (56). Delays of snowmelt date, for example, have led to delays in the hibernation emergence date of ground squirrels in Canada (33).

Threats and Opportunities from Regional Climate Change

Shifts in the regional distribution of climates can affect the availability and distribution of climati-

cally suitable areas for species across time and space (41). Increases or decreases in the area of climatic conditions that are suitable for species can lead to range expansions or contractions. Long-term ecological data reveal that species' distributions and abundances in both Northern and Southern Hemispheres often match, with time lag, warming and cooling cycles (57–60). Alpine trees (61) and other cold-adapted species of birds and butterflies (8), and small mammals like the mountain beaver and the western pocket gopher (62), for example, became confined to small and isolated pockets of cool conditions as the end of the last glacial period brought warmer temperatures. Climatic changes have also helped to explain range reductions of large mammals toward the end of the Late Quaternary (63). Indeed, continents losing more area representative of cold and dry conditions owing to climate changes during that period witnessed more extinctions of megafauna (21). By contrast, the extensive fossil record in North America and Eurasia provides evidence of increases in the distribution or abundance of plant species like elm and pine (64) and expansion of oaks out of glacial refugia (65) during the warming period of the last glacial. Contemporary changes have also been observed in high-latitude terrestrial ecosystems, where reduced ice-field extent has exposed new terrain for colonization and range expansion (66).

In turn, shifts in the position of climatic conditions affect the ability with which species track climatic conditions (67), and modulate the risk of range fragmentation. The magnitude of the Late Quaternary megafaunal extinctions discussed above was also greater in continents where suitable cold and dry conditions retreated farther (21). Over more recent decades, average range shifts observed for various taxonomic groups, mostly in the Northern Hemisphere, generally matched expectations from the poleward displacement of isotherms, despite variation in responses among species (54, 68). Differences and delays in responses (69) can partly result from barriers to dispersal imposed by habitat fragmentation (70) or unsuitable climate across time or space (71, 72), and can be stronger in lowland areas (73). Analyzing the direction to analogous climates can help to identify dispersal challenges as well as buffers, whereas the velocity of climate change provides an indication of the dispersal rates required to track suitable climates across the surrounding topography (74). In eastern North America, for example, the rate of northward shifts in the distribution of woody taxa populations over the last 16,000 years was paced by the velocity of temperature changes (20). The coincidence of global diversity patterns for amphibians, mammals and birds, and areas of low-velocity temperature change since the Last Glacial Maximum, 21,000 years ago, further illustrates the potential role of climate tracking for in situ persistence of species, particularly less vagile ones (16).

Predicting the effects of climate change on whole assemblages of species remains challenging.

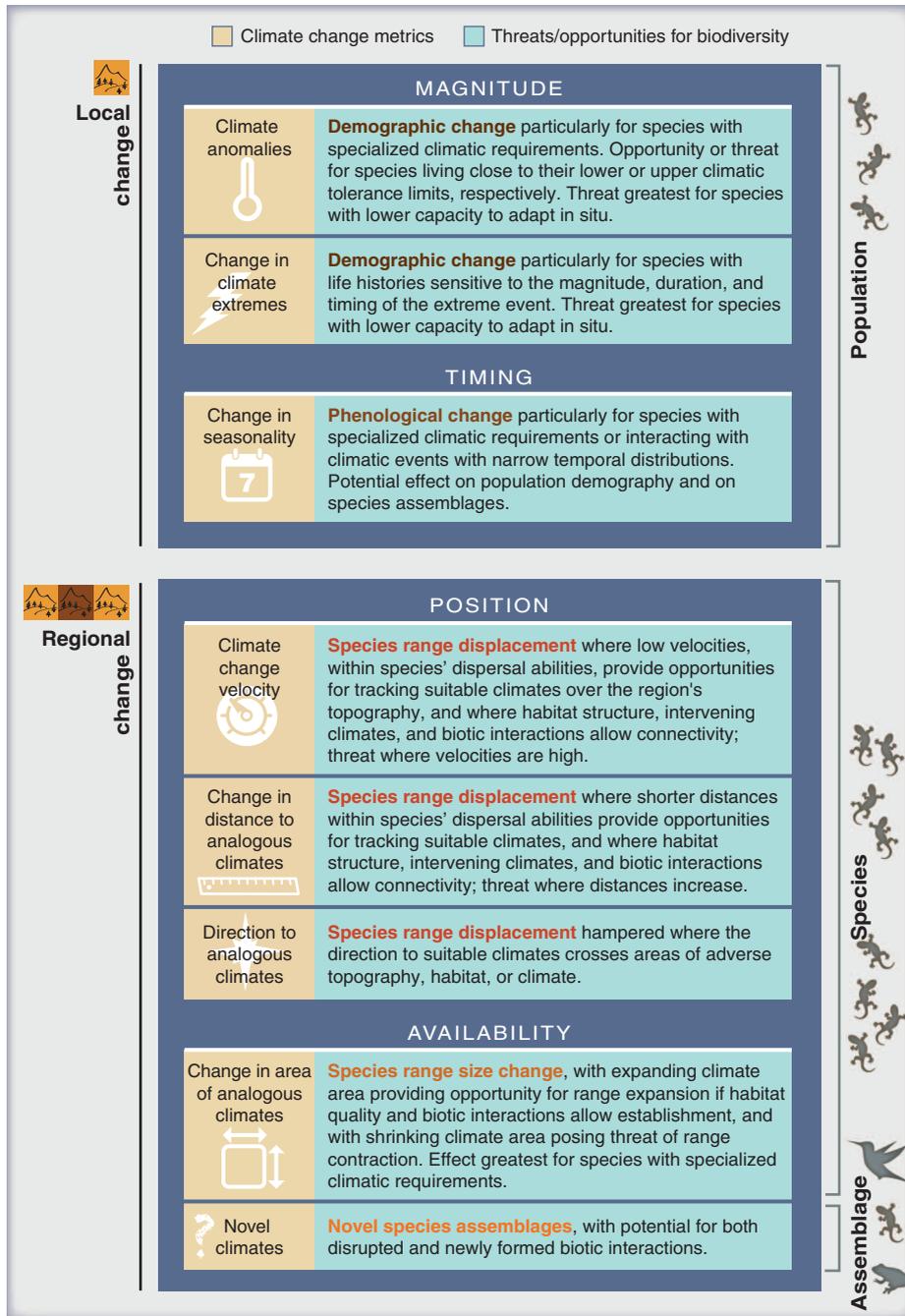


Fig. 3. Metrics of climate change and associated threats and opportunities for species. Metrics of climate change are grouped into four dimensions of change, and they either quantify changes at local (locality) level or at regional (set of localities) level (see Box 1). Links are established between metrics and potential threats and opportunities for population dynamics, species occurrence, and species assemblages.

Novel climates have been suggested to be associated with species assemblages also lacking modern analogs (75). One documented example is that of nonanalog vegetation assemblages in late-glacial eastern North America, which coincided with climatic conditions different from those occurring today (76, 77). In turn, disappearing climates can lead to the disaggregation of extant assemblages (23). In general, spatiotemporal shifts in the distribution of climate can result in the rearrangement of assemblages, with potential implications for species interactions and community reshuffling. Nonanalog communities (23, 78) can arise under changing climates either when species' individualistic responses lead to the disruption of existing interactions, or when species with nonoverlapping ranges come into contact and interact with one another (53, 79, 80). Examples include the climate-induced spread of pathogens (81, 82) or invasive species (83), decline of prey

species (84), and disruption of synchronization between different trophic levels (85). When exposed to extreme climates, communities can also switch into alternative ecological states (46, 86). Despite the complexity of community dynamics under climate change, measuring the multiple dimensions of climate change and their likely consequences for individual species (Fig. 3) is a first step toward a better understanding of the potential threats and opportunities for biodiversity.

The Limits of Climate Change Metrics

Linking multiple dimensions of climate change to threats and opportunities for species is only a first step toward understanding the effects of climate change on biodiversity. Ultimately, the effects of climate change on organisms are also dependent on their intrinsic abilities to cope with, or adapt to, the different challenges they face (87). Although climate change metrics can be

used as proxies for the threats and opportunities facing biodiversity, a number of considerations relating to the properties of individual species and the environment in which they live are important when interpreting metric outputs (see also Fig. 3). A first consideration is that climatic threats and opportunities do not act in isolation, but rather interact with other human-induced, ongoing threats (2). Notably, human-dominated landscapes (88) are an obstacle to species' dispersal and establishment, hampering opportunities to track suitable climates.

A second consideration when using metrics of climate change in biodiversity assessments is that the vulnerability of species to a given threat, or the capacity to seize a given opportunity, will vary across species. For example, individuals with higher genetic diversity, or higher capacity to change key morphological, physiological, or behavioral traits in response to adverse local

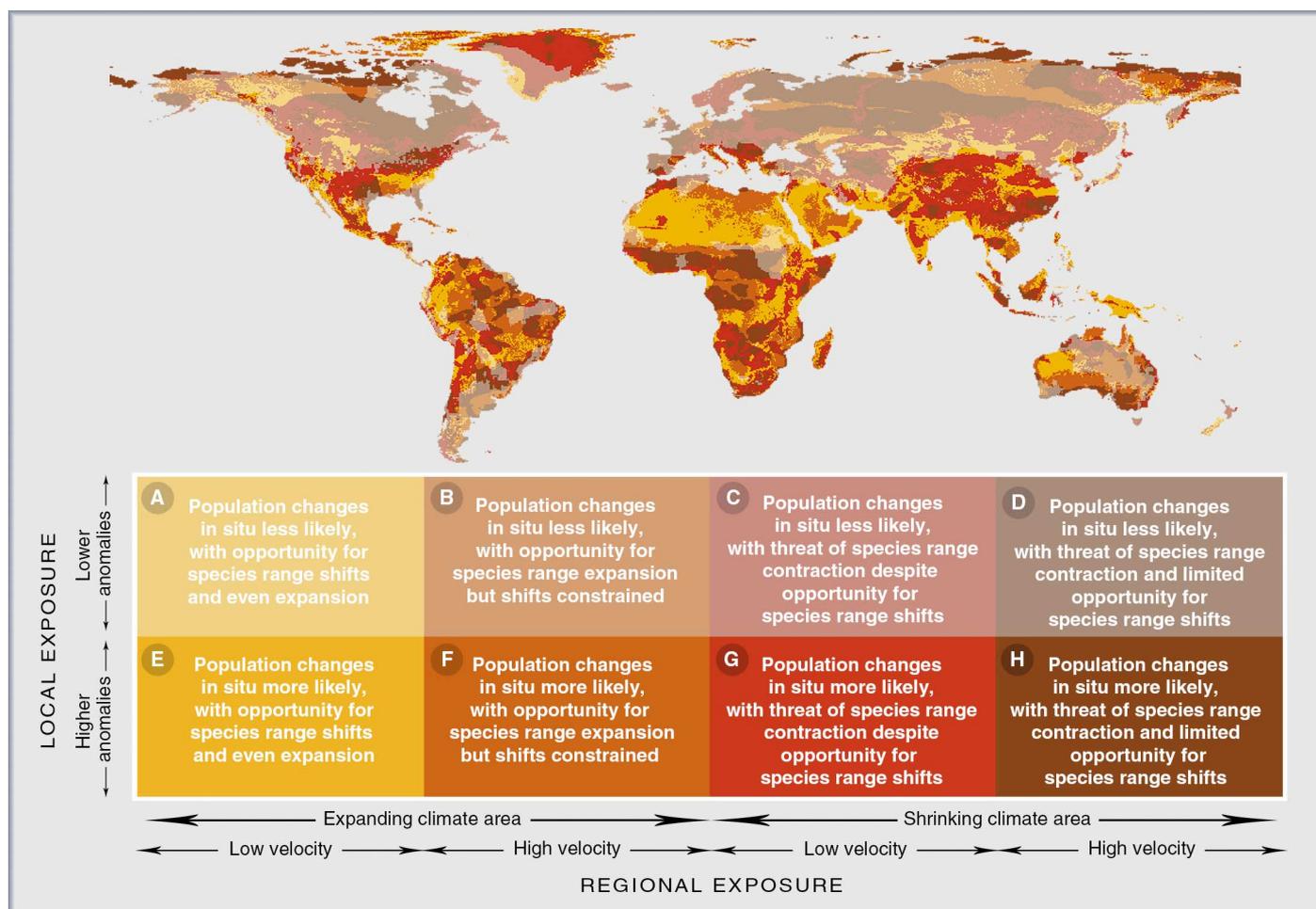


Fig. 4. Spatial overlap of climate change metrics. The three metrics selected as illustration—standardized local anomalies, change in area of baseline-analogous climates, and climate change velocity (120)—relate to different climate-induced threats and opportunities for biodiversity (Fig. 3). To account for species' potential dispersal limitations, changes in area of baseline-analogous climates were calculated by restricting the pool of climatic analogs to cells within 500 km from each cell (23). For each metric, two classes of values were defined. For anomalies, the two classes of values above and below the median denote higher and lower chances of demographic changes, respectively.

For changes in area, the two classes of positive and negative values correspond to opportunity for species range expansion and threat of range contraction, respectively. For velocity, the two classes of values above and below the median denote difficulty and opportunity for range displacement, respectively. The different shades on the map reflect the interaction between the three metrics overlaid in space, with the inferences about potential threats and opportunities for biodiversity dependent on species' and landscape characteristics (see Fig. 3). See fig. S6 for analysis of sensitivity to alternative climate models and fig. S7 for alternative combinations of climate change metrics.

climate changes, are better equipped to persist in situ under local climate change (87). Faced with extreme climate events, individuals with life histories more sensitive to the duration and magnitude of such events also face greater threat (45). Likewise, changes in the regional distribution of climates can disproportionately affect species with more specialized climatic requirements, as such species need to follow suitable climatic conditions more closely (8, 23). Where suitable climates are displaced, dispersal challenges will be greater for poor-dispersing and slow-reproducing species (89, 90).

Species also respond to different climate parameters (91), and such variability should be considered when interpreting climate change metrics. As the spatial patterns arising from a given metric vary between temperature and precipitation, for example [(19, 92) and this review], the threats and opportunities inferred from metrics may affect individual species differently depending on which parameter is measured. Finally, the temporal and spatial scales at which climate changes are measured are also important (93, 94). Climatic thresholds for the survival or reproduction of individuals, often mediating population demographic changes, vary across seasons and life-history stages (93). Likewise, the effect of extreme events of a given magnitude and duration is best assessed relative to the life cycles of organisms (45). Changes measured over long time frames can also conceal fine-scale climatic variability that drives pulses of expansion or contraction in species' ranges, as has been shown for North American trees during the Holocene (95). Likewise, climatic changes quantified at coarse spatial resolutions can overlook microrefugia and thereby overestimate risks. Evidence exists that such refugia have enabled species to persist through periods of climate change, especially those with small home ranges (96). The relevant spatial extent for calculating regional metrics may also vary across species with different dispersal abilities (23). For example, broad regional pools of climates may be accessible to vagile species, but not to poor dispersers.

A Combined View of Threats and Opportunities

Given that alternative metrics reveal contrasting spatial patterns (Fig. 1) and represent different threats and opportunities for species (Fig. 3), how should they be used in assessments of climate change impacts on biodiversity? Single metrics of climate change have been used to predict the degree to which global biodiversity will be exposed to extreme climates at the locality level (10), to reduced availability of similar climates worldwide (23) or within ecoregions (11), or to high velocities of climate displacement across the surrounding topography (9). Although individual dimensions of change may be critical for particular species, they each provide only one facet of the many climatic challenges facing biodiversity. For example, mapping climate anomalies reveals where populations may potentially be most threatened

with demographic changes, but not where opportunities may arise for organisms to track moving climates. Likewise, a map of the future availability of climatic conditions contains no information about how accessible such conditions are to species.

In principle, threats or opportunities for biodiversity should increase where species are simultaneously exposed to several dimensions of climate change (2, 97). Examining multiple metrics in combination can show how dimensions of climate change interact among themselves to exacerbate or lessen species' exposure to climate change. The selection of metrics is contingent on the question, but should cover all dimensions of change deemed relevant. For illustration, we considered three metrics quantifying alternative dimensions of climate change: standardized anomalies, change in area of neighboring analogous climates (23), and climate change velocity. These metrics are expected to relate to local demographic changes, species' range contractions or expansions, and species' range displacements, respectively (Fig. 3). Spatially overlaying the selected metrics worldwide (Fig. 4) highlights the interactions among dimensions of climate change across broad geographical areas. However, how such changes will translate into threats and opportunities for biodiversity is likely perceived differently across species (Fig. 3).

Nearly 11% of the global land surface is exposed to large changes in the three metrics examined, mostly in the Nordic tundra and tropical areas [shade (H) in Fig. 4]. Both positive and negative effects of local warming have been reported on population dynamics in high-latitude areas (50, 51, 98). Species with wide tolerance to the environmental variability that is typical of such areas (99), or with access to microrefugia, are better equipped to cope with adverse changes. Yet, at the spatial scale used here, the high velocities required to track polar climates in the future compound the regional shrinkage of these climates, placing polar species under the threat of range contraction.

Mountain areas offer more opportunities for species to track slow-moving climates over the complex mosaic of microclimates provided by the local topography (94). However, range contraction still appears as a threat at the regional level [shade (G) in Fig. 4]. Where suitable climates disappear altogether within the species' reach, threat of extinction from habitat and ecosystem loss will be greater for species endemic to those climates (8, 23). Small-ranged species of tropical mountain areas with high levels of endemism, and species lacking the genetic variability to survive in remnant isolated populations (100), thus appear particularly threatened. Species in cold climate areas of the Northern Hemisphere face similar decreases in availability of suitable climates [shades (C) and (D) in Fig. 4]. In such areas, local anomalies pose smaller threats relative to the historical interannual variability, but at the regional level, species that are specialized on these cold climates might face the threat of range contraction. Where the velocity of climate displacement is

high [shade (D) in Fig. 4], or where landscapes are highly modified, dispersal challenges will also be greater.

By contrast, most of the remaining tropical and subtropical regions are exposed to climates that are expanding regionally as well as changing locally [shades (E) and (F) in Fig. 4]. If tropical species require specialized climatic conditions, or live closer to their upper tolerance limits, as seems often to be the case (101, 102), then they are likely threatened by local changes because phenotypic plasticity (103) and physiological adaptation (104) are reduced in such circumstances. Faced with local changes, species in areas of low climate velocities have greater opportunities for adaptation through dispersal [shade (E) in Fig. 4], particularly if such species are poor dispersers. By contrast, the shallower latitudinal gradients of temperature (105) of the lowlands of the Amazon and Congo Basin, for example, may prevent dispersal and expansion into newly suitable areas [shade (F) in Fig. 4].

Challenges for Impact Assessment and Conservation

No single unifying metric of climate change exists. The conceptual framework proposed here can help interpreting the outputs of different metrics by classifying them into common currencies of threat and opportunity. Although the framework can be applied to a range of sectors, including agriculture, forestry and health, our focus is on impacts of climate change on biodiversity.

Projecting the level of exposure of biodiversity to climatic changes is an integral part of any framework to assess risks and select appropriate conservation strategies. Some of the existing frameworks for conservation under changing climates rely on single metrics of climate change as proxies for exposure, including the velocity of climate change (106), local anomalies (107), and the availability of climatic conditions (11). Whereas each of these frameworks addresses conservation needs in the face of specific threats and opportunities for biodiversity, integrating multiple metrics into a single framework would allow for the identification of complementary conservation strategies. For example, mitigating local impacts through abatement of habitat loss and enhancement of habitat quality or heterogeneity (108) can be vital in areas where shrinking climates reduce opportunities for species survival outside present ranges, particularly for climatically specialized species. By contrast, promoting landscape connectivity (109) and restoring new target habitat will be warranted wherever local changes threaten in situ persistence but low velocities of climate change enable species to track suitable climates.

The actual effects of climate change on biodiversity are extremely difficult to predict owing to the complexity of species and community dynamics, in addition to the interaction with other stressors. Climate change metrics do not account for intrinsic responses of species to climatic and other changes and are affected by the uncertainty

of the underlying climate data. Yet, metrics are likely to remain an important assessment tool for at least three reasons. First, models assessing the effects of climate change on biodiversity are typically calibrated to average climates, and little attention has been paid to alternative dimensions of local change such as climatic extremes or the timing of climatic events. Teasing apart alternative dimensions of change to complement model-based assessments, or integrating them into models (110, 111), can bring valuable additional information.

Second, metrics can be used for assessing climate change exposure when insufficient data are available on the distributions of species. Such is the case for the majority of known species across taxa (112), and particularly for the species-rich and highly impacted tropical areas (113). Research on climate change impacts for biodiversity has to date been geographically and taxonomically biased (114), often excluding cryptic species and those that are currently most threatened owing to lack of sufficient data points for modeling. Hence, it is not a trivial feature of metric-based assessments that they can be applied when and where limited knowledge of biodiversity exists.

Third, the sheer number of underdescribed and undiscovered species (115) means that assessments relying on available data represent a very small proportion of the total existing biodiversity. For example, global inventories are estimated to cover only 20% of all existing insects (115), a group with considerable influence on ecosystem functioning and services. When carefully implemented and linked to threats and opportunities, simple metrics of climate change can provide a first-order assessment of the potential effects on the biota as a whole.

References and Notes

- G.-R. Walther *et al.*, Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002). doi: [10.1038/416389a](https://doi.org/10.1038/416389a); pmid: [11919621](https://pubmed.ncbi.nlm.nih.gov/11919621/)
- B. W. Brook, N. S. Sodhi, C. J. A. Bradshaw, Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460 (2008). doi: [10.1016/j.tree.2008.03.011](https://doi.org/10.1016/j.tree.2008.03.011); pmid: [18582986](https://pubmed.ncbi.nlm.nih.gov/18582986/)
- H. M. Pereira *et al.*, Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501 (2010). doi: [10.1126/science.1196624](https://doi.org/10.1126/science.1196624); pmid: [20978282](https://pubmed.ncbi.nlm.nih.gov/20978282/)
- S. M. McMahon *et al.*, Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends Ecol. Evol.* **26**, 249–259 (2011). doi: [10.1016/j.tree.2011.02.012](https://doi.org/10.1016/j.tree.2011.02.012); pmid: [21474198](https://pubmed.ncbi.nlm.nih.gov/21474198/)
- A. T. Peterson *et al.*, *Ecological Niches and Geographic Distributions* (Monographs in Population Biology, Princeton Univ. Press, Princeton, NJ, 2011).
- D. A. Keith *et al.*, Predicting extinction risks under climate change: Coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* **4**, 560–563 (2008). doi: [10.1098/rsbl.2008.0049](https://doi.org/10.1098/rsbl.2008.0049); pmid: [18664424](https://pubmed.ncbi.nlm.nih.gov/18664424/)
- M. Kearney, W. Porter, Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **12**, 334–350 (2009). doi: [10.1111/j.1461-0248.2008.01277.x](https://doi.org/10.1111/j.1461-0248.2008.01277.x); pmid: [19292794](https://pubmed.ncbi.nlm.nih.gov/19292794/)
- R. Ohlemüller *et al.*, The coincidence of climatic and species rarity: High risk to small-range species from climate change. *Biol. Lett.* **4**, 568–572 (2008). doi: [10.1098/rsbl.2008.0097](https://doi.org/10.1098/rsbl.2008.0097); pmid: [18664421](https://pubmed.ncbi.nlm.nih.gov/18664421/)
- S. R. Loarie *et al.*, The velocity of climate change. *Nature* **462**, 1052–1055 (2009). doi: [10.1038/nature08649](https://doi.org/10.1038/nature08649); pmid: [20033047](https://pubmed.ncbi.nlm.nih.gov/20033047/)
- L. J. Beaumont *et al.*, Impacts of climate change on the world's most exceptional ecoregions. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 2306–2311 (2011). doi: [10.1073/pnas.1007217108](https://doi.org/10.1073/pnas.1007217108); pmid: [21262825](https://pubmed.ncbi.nlm.nih.gov/21262825/)
- J. E. M. Watson, T. Iwamura, N. Butt, Mapping vulnerability and conservation adaptation strategies under climate change. *Nat. Clim. Change* **3**, 989–994 (2013). doi: [10.1038/nclimate2007](https://doi.org/10.1038/nclimate2007)
- M. B. Araújo *et al.*, Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography* **31**, 8–15 (2008). doi: [10.1111/j.2007.0906-7590.05318.x](https://doi.org/10.1111/j.2007.0906-7590.05318.x)
- M. T. Burrows *et al.*, The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652–655 (2011). doi: [10.1126/science.1210288](https://doi.org/10.1126/science.1210288); pmid: [22053045](https://pubmed.ncbi.nlm.nih.gov/22053045/)
- J. Hortal *et al.*, Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecol. Lett.* **14**, 741–748 (2011). doi: [10.1111/j.1461-0248.2011.01634.x](https://doi.org/10.1111/j.1461-0248.2011.01634.x); pmid: [21645193](https://pubmed.ncbi.nlm.nih.gov/21645193/)
- S. F. Gouveia, J. Hortal, F. S. Cassemiro, T. F. Rangel, J. A. F. Diniz-Filho, Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography* **36**, 104–113 (2013). doi: [10.1111/j.1600-0587.2012.07553.x](https://doi.org/10.1111/j.1600-0587.2012.07553.x)
- B. Sandel *et al.*, The influence of Late Quaternary climate-change velocity on species endemism. *Science* **334**, 660–664 (2011). doi: [10.1126/science.1210173](https://doi.org/10.1126/science.1210173); pmid: [21979937](https://pubmed.ncbi.nlm.nih.gov/21979937/)
- M. B. Ashcroft, J. R. Gollan, D. I. Warton, D. Ramp, A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Glob. Change Biol.* **18**, 1866–1879 (2012). doi: [10.1111/j.1365-2486.2012.02661.x](https://doi.org/10.1111/j.1365-2486.2012.02661.x)
- F. P. Werneck, C. Nogueira, G. R. Colli, J. W. Sites Jr., G. C. Costa, Climatic stability in the Brazilian Cerrado: Implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *J. Biogeogr.* **39**, 1695–1706 (2012). doi: [10.1111/j.1365-2699.2012.02715.x](https://doi.org/10.1111/j.1365-2699.2012.02715.x)
- J. VanDerWal *et al.*, Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nat. Clim. Change* **3**, 239–243 (2013). doi: [10.1038/nclimate1688](https://doi.org/10.1038/nclimate1688)
- A. Ordóñez, J. W. Williams, Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecol. Lett.* **16**, 773–781 (2013). doi: [10.1111/ele.12110](https://doi.org/10.1111/ele.12110); pmid: [23574198](https://pubmed.ncbi.nlm.nih.gov/23574198/)
- D. Nogués-Bravo, R. Ohlemüller, P. Batra, M. B. Araújo, Climate predictors of late quaternary extinctions. *Evolution* **64**, 2442–2449 (2010). pmid: [20707809](https://pubmed.ncbi.nlm.nih.gov/20707809/)
- B. Dalsgaard *et al.*, Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. *PLOS ONE* **6**, e25891 (2011). doi: [10.1371/journal.pone.0025891](https://doi.org/10.1371/journal.pone.0025891); pmid: [21998716](https://pubmed.ncbi.nlm.nih.gov/21998716/)
- J. W. Williams, S. T. Jackson, J. E. Kutzbach, Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 5738–5742 (2007). doi: [10.1073/pnas.0606292104](https://doi.org/10.1073/pnas.0606292104); pmid: [17389402](https://pubmed.ncbi.nlm.nih.gov/17389402/)
- C. D. Thomas *et al.*, Exporting the ecological effects of climate change. Developed and developing countries will suffer the consequences of climate change, but differ in both their responsibility and how badly it will affect their ecosystems. *EMBO Rep.* **9** (suppl. 1), S28–S33 (2008). doi: [10.1038/embor.2008.42](https://doi.org/10.1038/embor.2008.42); pmid: [18578020](https://pubmed.ncbi.nlm.nih.gov/18578020/)
- S. J. Wright, H. C. Muller-Landau, J. Schipper, The future of tropical species on a warmer planet. *Conserv. Biol.* **23**, 1418–1426 (2009). doi: [10.1111/j.1523-1739.2009.01337.x](https://doi.org/10.1111/j.1523-1739.2009.01337.x); pmid: [20078642](https://pubmed.ncbi.nlm.nih.gov/20078642/)
- M. A. Jiménez *et al.*, Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities. *Ecol. Lett.* **14**, 1227–1235 (2011). doi: [10.1111/j.1461-0248.2011.01693.x](https://doi.org/10.1111/j.1461-0248.2011.01693.x); pmid: [21988736](https://pubmed.ncbi.nlm.nih.gov/21988736/)
- J. Li *et al.*, Global priority conservation areas in the face of 21st century climate change. *PLOS ONE* **8**, e54839 (2013). doi: [10.1371/journal.pone.0054839](https://doi.org/10.1371/journal.pone.0054839); pmid: [23359638](https://pubmed.ncbi.nlm.nih.gov/23359638/)
- T. Iwamura, K. A. Wilson, O. Venter, H. P. Possingham, A climatic stability approach to prioritizing global conservation investments. *PLOS ONE* **5**, e15103 (2010). doi: [10.1371/journal.pone.0015103](https://doi.org/10.1371/journal.pone.0015103); pmid: [21152095](https://pubmed.ncbi.nlm.nih.gov/21152095/)
- J. A. Wiens, N. E. Seavy, D. Jongsomjit, Protected areas in climate space: What will the future bring? *Biol. Conserv.* **144**, 2119–2125 (2011). doi: [10.1016/j.biocon.2011.05.002](https://doi.org/10.1016/j.biocon.2011.05.002)
- T. Iwamura, A. Guisan, K. A. Wilson, H. P. Possingham, How robust are global conservation priorities to climate change? *Glob. Environ. Change* **23**, 1277–1284 (2013). doi: [10.1016/j.gloenvcha.2013.07.016](https://doi.org/10.1016/j.gloenvcha.2013.07.016)
- J. Bergmann *et al.*, The Iberian Peninsula as a potential source for the plant species pool in Germany under projected climate change. *Plant Ecol.* **207**, 191–201 (2010). doi: [10.1007/s11258-009-9664-6](https://doi.org/10.1007/s11258-009-9664-6)
- F. Giorgi, Climate change hot-spots. *Geophys. Res. Lett.* **33**, L08707 (2006). doi: [10.1029/2006GL025734](https://doi.org/10.1029/2006GL025734)
- J. E. Lane, L. E. B. Kruuk, A. Charmanier, J. O. Murie, F. S. Dobson, Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* **489**, 554–557 (2012). doi: [10.1038/nature11335](https://doi.org/10.1038/nature11335); pmid: [22878721](https://pubmed.ncbi.nlm.nih.gov/22878721/)
- R. Ohlemüller, E. S. Gritti, M. T. Sykes, C. D. Thomas, Towards European climate risk surfaces: The extent and distribution of analogous and non-analogous climates 1931–2100. *Glob. Ecol. Biogeogr.* **15**, 395–405 (2006). doi: [10.1111/j.1466-822X.2006.00245.x](https://doi.org/10.1111/j.1466-822X.2006.00245.x)
- D. D. Ackerly *et al.*, The geography of climate change: Implications for conservation biogeography. *Divers. Distrib.* **16**, 476–487 (2010). doi: [10.1111/j.1472-4642.2010.00654.x](https://doi.org/10.1111/j.1472-4642.2010.00654.x)
- C. Tebaldi, K. Hayhoe, J. M. Arblaster, G. A. Meehl, Going to the Extremes. *Clim. Change* **79**, 185–211 (2006). doi: [10.1007/s10584-006-9051-4](https://doi.org/10.1007/s10584-006-9051-4)
- B. Orlowsky, S. Seneviratne, Global changes in extreme events: Regional and seasonal dimension. *Clim. Change* **110**, 669–696 (2012). doi: [10.1007/s10584-011-0122-9](https://doi.org/10.1007/s10584-011-0122-9)
- G. A. Meehl *et al.*, in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, S. Solomon *et al.*, Eds. (Cambridge Univ. Press, Cambridge, UK, and New York, 2007), chap. 10.
- L. R. Holdridge, Determination of world plant formations from simple climatic data. *Science* **105**, 367–368 (1947). doi: [10.1126/science.105.2727.367](https://doi.org/10.1126/science.105.2727.367); pmid: [17800882](https://pubmed.ncbi.nlm.nih.gov/17800882/)
- R. H. Whittaker, *Communities and ecosystems* (Macmillan, New York, ed. 2, 1975).
- S. T. Jackson, J. T. Overpeck, Responses of Plant Populations and Communities to Environmental Changes of the Late Quaternary. *Paleobiology* **26** (sp4), 194–220 (2000). doi: [10.1666/0094-8373\(2000\)26\[194:ROPPAC\]2.0.CO;2](https://doi.org/10.1666/0094-8373(2000)26[194:ROPPAC]2.0.CO;2)
- J. Peñuelas *et al.*, Evidence of current impact of climate change on life: A walk from genes to the biosphere. *Glob. Change Biol.* **19**, 2303–2338 (2013). doi: [10.1111/gcb.12143](https://doi.org/10.1111/gcb.12143); pmid: [23505157](https://pubmed.ncbi.nlm.nih.gov/23505157/)
- B. Sinervo *et al.*, Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899 (2010). doi: [10.1126/science.1184695](https://doi.org/10.1126/science.1184695); pmid: [20466932](https://pubmed.ncbi.nlm.nih.gov/20466932/)
- W. Foden *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). doi: [10.1111/j.1472-4642.2007.00391.x](https://doi.org/10.1111/j.1472-4642.2007.00391.x)
- A. Jentsch, J. Kreyling, C. Beierkuhnlein, A new generation of climate-change experiments: Events, not trends. *Front. Ecol. Environ* **5**, 365–374 (2007). doi: [10.1890/1540-9295\(2007\)5\[365:ANGOC\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[365:ANGOC]2.0.CO;2)
- A. Jentsch, C. Beierkuhnlein, Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *C. R. Geosci.* **340**, 621–628 (2008). doi: [10.1016/j.crte.2008.07.002](https://doi.org/10.1016/j.crte.2008.07.002)
- C. D. Allen *et al.*, A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* **259**, 660–684 (2010). doi: [10.1016/j.foreco.2009.09.001](https://doi.org/10.1016/j.foreco.2009.09.001)
- S. Chamaillet-Jammes, M. Massot, P. Aragón, J. Clobert, Global warming and positive fitness response in mountain populations of common lizards *Lacerta*

- vivipara. *Glob. Change Biol.* **12**, 392–402 (2006). doi: [10.1111/j.1365-2486.2005.01088.x](https://doi.org/10.1111/j.1365-2486.2005.01088.x)
49. J. A. Fowbert, R. I. L. Smith, Rapid Population Increases in Native Vascular Plants in the Argentine Islands, Antarctic Peninsula. *Arct. Alp. Res.* **26**, 290–296 (1994). doi: [10.2307/1551941](https://doi.org/10.2307/1551941)
50. G. B. Hill, G. H. R. Henry, Responses of High Arctic wet sedge tundra to climate warming since 1980. *Glob. Change Biol.* **17**, 276–287 (2011). doi: [10.1111/j.1365-2486.2010.02244.x](https://doi.org/10.1111/j.1365-2486.2010.02244.x)
51. N. J. C. Tyler, M. C. Forchhammer, N. A. Øritsland, Nonlinear effects of climate and density in the dynamics of a fluctuating population of reindeer. *Ecology* **89**, 1675–1686 (2008). doi: [10.1890/07-0416.1](https://doi.org/10.1890/07-0416.1); pmid: [18589531](https://pubmed.ncbi.nlm.nih.gov/18589531/)
52. A. J. Miller-Rushing, T. T. Høye, D. W. Inouye, E. Post, The effects of phenological mismatches on demography. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 3177–3186 (2010). doi: [10.1098/rstb.2010.0148](https://doi.org/10.1098/rstb.2010.0148); pmid: [20819811](https://pubmed.ncbi.nlm.nih.gov/20819811/)
53. E. Post, *Ecology of Climate Change. The Importance of Biotic Interactions* (Princeton Univ. Press, Princeton, NJ, 2013).
54. C. Parmesan, G. Yohe, A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003). doi: [10.1038/nature01286](https://doi.org/10.1038/nature01286); pmid: [12511946](https://pubmed.ncbi.nlm.nih.gov/12511946/)
55. T. L. Root *et al.*, Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60 (2003). doi: [10.1038/nature01333](https://doi.org/10.1038/nature01333); pmid: [12511952](https://pubmed.ncbi.nlm.nih.gov/12511952/)
56. A. Jentsch, J. Kreyling, J. Boettcher-Treschkow, C. Beierkuhnlein, Beyond gradual warming: Extreme weather events alter flower phenology of European grassland and heath species. *Glob. Change Biol.* **15**, 837–849 (2009). doi: [10.1111/j.1365-2486.2008.01690.x](https://doi.org/10.1111/j.1365-2486.2008.01690.x)
57. L. R. Flenley, Tropical forests under the climates of the last 30,000 Years. *Clim. Change* **39**, 177–197 (1998). doi: [10.1023/A:1005367822750](https://doi.org/10.1023/A:1005367822750)
58. R. J. Morley, M. Bush, J. Flenley, W. Gosling, in *Tropical Rainforest Responses to Clim. Change*, M. B. Bush, J. R. Flenley, W. D. Gosling, Eds. (Springer, Berlin and Heidelberg, Germany, 2011), pp. 1–34.
59. K. J. Willis, G. M. MacDonald, Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annu. Rev. Ecol. Syst.* **42**, 267–287 (2011). doi: [10.1146/annurev-ecolsys-102209-144704](https://doi.org/10.1146/annurev-ecolsys-102209-144704)
60. K. J. Willis, K. D. Bennett, S. L. Burrough, N. Macias-Fauria, C. Tovar, Determining the response of African biota to climate change: Using the past to model the future. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120491 (2013). doi: [10.1098/rstb.2012.0491](https://doi.org/10.1098/rstb.2012.0491); pmid: [23878343](https://pubmed.ncbi.nlm.nih.gov/23878343/)
61. H. J. B. Birks, K. J. Willis, Alpines, trees, and refugia in Europe. *Plant Ecol. Divers.* **1**, 147–160 (2008). doi: [10.1080/17550870802349146](https://doi.org/10.1080/17550870802349146)
62. J. L. Blois, J. L. McGuire, E. A. Hadly, Small mammal diversity loss in response to late-Pleistocene climatic change. *Nature* **465**, 771–774 (2010). doi: [10.1038/nature09077](https://doi.org/10.1038/nature09077); pmid: [20495547](https://pubmed.ncbi.nlm.nih.gov/20495547/)
63. E. D. Lorenzen *et al.*, Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* **479**, 359–364 (2011). doi: [10.1038/nature10574](https://doi.org/10.1038/nature10574); pmid: [22048313](https://pubmed.ncbi.nlm.nih.gov/22048313/)
64. J. W. Williams, B. N. Shuman, T. Webb III, P. J. Bartlein, P. L. Leduc, Late-Quaternary vegetation dynamics in North America: Scaling from taxa to biomes. *Ecol. Monogr.* **74**, 309–334 (2004). doi: [10.1890/02-4045](https://doi.org/10.1890/02-4045)
65. M. B. Davis, R. G. Shaw, Range shifts and adaptive responses to Quaternary climate change. *Science* **292**, 673–679 (2001). doi: [10.1126/science.292.5517.673](https://doi.org/10.1126/science.292.5517.673); pmid: [11326089](https://pubmed.ncbi.nlm.nih.gov/11326089/)
66. P. Convey, R. I. Smith, Responses of terrestrial Antarctic ecosystems to climate change. *Plant Ecol.* **182**, 1–10 (2006).
67. L. F. Pitelka *et al.*, Plant migration and climate change. *Am. Sci.* **85**, 464–474 (1997).
68. I.-C. Chen, J. K. Hill, R. Ohlemüller, D. B. Roy, C. D. Thomas, Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011). doi: [10.1126/science.1206432](https://doi.org/10.1126/science.1206432); pmid: [21852500](https://pubmed.ncbi.nlm.nih.gov/21852500/)
69. M. B. Davis, in *Community Ecology*, J. Diamond, T. J. Case, Eds. (Harper and Row, 1986), pp. 269–284.
70. J. K. Hill *et al.*, Impacts of landscape structure on butterfly range expansion. *Ecol. Lett.* **4**, 313–321 (2001). doi: [10.1046/j.1461-0248.2001.00222.x](https://doi.org/10.1046/j.1461-0248.2001.00222.x)
71. R. Early, D. F. Sax, Analysis of climate paths reveals potential limitations on species range shifts. *Ecol. Lett.* **14**, 1125–1133 (2011). doi: [10.1111/j.1461-0248.2011.01681.x](https://doi.org/10.1111/j.1461-0248.2011.01681.x); pmid: [21955643](https://pubmed.ncbi.nlm.nih.gov/21955643/)
72. J. Bennie *et al.*, Range expansion through fragmented landscapes under a variable climate. *Ecol. Lett.* **16**, 921–929 (2013). doi: [10.1111/ele.12129](https://doi.org/10.1111/ele.12129); pmid: [23701124](https://pubmed.ncbi.nlm.nih.gov/23701124/)
73. R. Bertrand *et al.*, Changes in plant community composition lag behind climate warming in lowland forests. *Nature* **479**, 517–520 (2011). doi: [10.1038/nature10548](https://doi.org/10.1038/nature10548); pmid: [22012261](https://pubmed.ncbi.nlm.nih.gov/22012261/)
74. D. L. Peterson, E. G. Schreiner, N. M. Buckingham, Gradients, vegetation and climate: Spatial and temporal dynamics in the Olympic Mountains, U.S.A. *Global Ecol. Biogeogr. Lett.* **6**, 7–17 (1997). doi: [10.2307/2997523](https://doi.org/10.2307/2997523)
75. J. W. Williams, S. T. Jackson, Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ* **5**, 475–482 (2007). doi: [10.1890/070037](https://doi.org/10.1890/070037)
76. J. W. Williams, B. N. Shuman, I. I. T. Webb, Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology* **82**, 3346–3362 (2001).
77. J. T. Overpeck, R. S. Webb, T. Webb III, Mapping eastern North American vegetation change of the past 18 ka: No-analogs and the future. *Geology* **20**, 1071–1074 (1992). doi: [10.1130/0091-7613\(1992\)020<1071: MENAVC>2.3.CO;2](https://doi.org/10.1130/0091-7613(1992)020<1071: MENAVC>2.3.CO;2)
78. R. W. Graham *et al.*, Spatial response of mammals to late Quaternary environmental fluctuations. *Science* **272**, 1601–1606 (1996). doi: [10.1126/science.272.5268.1601](https://doi.org/10.1126/science.272.5268.1601); pmid: [8662471](https://pubmed.ncbi.nlm.nih.gov/8662471/)
79. E. Post *et al.*, Ecological dynamics across the Arctic associated with recent climate change. *Science* **325**, 1355–1358 (2009). doi: [10.1126/science.1173113](https://doi.org/10.1126/science.1173113); pmid: [19745143](https://pubmed.ncbi.nlm.nih.gov/19745143/)
80. G.-R. Walther, Community and ecosystem responses to recent climate change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2019–2024 (2010). doi: [10.1098/rstb.2010.0021](https://doi.org/10.1098/rstb.2010.0021); pmid: [20513710](https://pubmed.ncbi.nlm.nih.gov/20513710/)
81. J. A. Pounds *et al.*, Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167 (2006). doi: [10.1038/nature04246](https://doi.org/10.1038/nature04246); pmid: [16407945](https://pubmed.ncbi.nlm.nih.gov/16407945/)
82. J. R. Rohr, T. R. Raffel, Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 8269–8274 (2010). doi: [10.1073/pnas.0912883107](https://doi.org/10.1073/pnas.0912883107); pmid: [20404180](https://pubmed.ncbi.nlm.nih.gov/20404180/)
83. J. M. Diez *et al.*, Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ* **10**, 249–257 (2012). doi: [10.1890/110137](https://doi.org/10.1890/110137)
84. I. Durance, S. J. Ormerod, Evidence for the role of climate in the local extinction of a cool-water triclad. *J. N. Am. Benthol. Soc.* **29**, 1367–1378 (2010). doi: [10.1899/09-159.1](https://doi.org/10.1899/09-159.1)
85. M. E. Visser, L. J. M. Holleman, Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 289–294 (2001). doi: [10.1098/rspb.2000.1363](https://doi.org/10.1098/rspb.2000.1363); pmid: [11217900](https://pubmed.ncbi.nlm.nih.gov/11217900/)
86. M. Scheffer, S. Carpenter, J. A. Foley, C. Folke, B. Walker, Catastrophic shifts in ecosystems. *Nature* **413**, 591–596 (2001). doi: [10.1038/35098000](https://doi.org/10.1038/35098000); pmid: [11595939](https://pubmed.ncbi.nlm.nih.gov/11595939/)
87. L.-M. Chevin, R. Lande, G. M. Mace, Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLOS Biol.* **8**, e1000357 (2010). doi: [10.1371/journal.pbio.1000357](https://doi.org/10.1371/journal.pbio.1000357); pmid: [20463950](https://pubmed.ncbi.nlm.nih.gov/20463950/)
88. E. C. Ellis, N. Ramankutty, Putting people in the map: Anthropogenic biomes of the world. *Front. Ecol. Environ* **6**, 439–447 (2008). doi: [10.1890/070062](https://doi.org/10.1890/070062)
89. A. L. Angert *et al.*, Do species' traits predict recent shifts at expanding range edges? *Ecol. Lett.* **14**, 677–689 (2011). doi: [10.1111/j.1461-0248.2011.01620.x](https://doi.org/10.1111/j.1461-0248.2011.01620.x); pmid: [21535340](https://pubmed.ncbi.nlm.nih.gov/21535340/)
90. C. A. Schloss, T. A. Nuñez, J. J. Lawler, Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 8606–8611 (2012). doi: [10.1073/pnas.1116791109](https://doi.org/10.1073/pnas.1116791109); pmid: [22586104](https://pubmed.ncbi.nlm.nih.gov/22586104/)
91. M. W. Tingley, W. B. Monahan, S. R. Beissinger, C. Moritz, Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci. U.S.A.* **106** (suppl. 2), 19637–19643 (2009). doi: [10.1073/pnas.0901562106](https://doi.org/10.1073/pnas.0901562106); pmid: [19805037](https://pubmed.ncbi.nlm.nih.gov/19805037/)
92. A. Ordóñez, J. W. Williams, Projected climate reshuffling based on multivariate climate-availability, climate-analog, and climate-velocity analyses: Implications for community disaggregation. *Clim. Change* **119**, 659–675 (2013). doi: [10.1007/s10584-013-0752-1](https://doi.org/10.1007/s10584-013-0752-1)
93. S. T. Jackson, J. L. Betancourt, R. K. Booth, S. T. Gray, Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proc. Natl. Acad. Sci. U.S.A.* **106** (suppl. 2), 19685–19692 (2009). doi: [10.1073/pnas.0901641106](https://doi.org/10.1073/pnas.0901641106); pmid: [19805104](https://pubmed.ncbi.nlm.nih.gov/19805104/)
94. S. Z. Dobrowski, A climatic basis for microrefugia: The influence of terrain on climate. *Glob. Change Biol.* **17**, 1022–1035 (2011). doi: [10.1111/j.1365-2486.2010.02263.x](https://doi.org/10.1111/j.1365-2486.2010.02263.x)
95. S. T. Gray, J. L. Betancourt, S. T. Jackson, R. G. Eddy, Role of multidecadal climate variability in a range extension of pinyon pine. *Ecology* **87**, 1124–1130 (2006). doi: [10.1890/0012-9658\(2006\)87\[1124:ROMCV\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1124:ROMCV]2.0.CO;2); pmid: [16761590](https://pubmed.ncbi.nlm.nih.gov/16761590/)
96. K. J. Willis, T. H. van Andel, Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat. Sci. Rev.* **23**, 2369–2387 (2004). doi: [10.1016/j.quascirev.2004.06.002](https://doi.org/10.1016/j.quascirev.2004.06.002)
97. C. Hof, M. B. Araújo, W. Jetz, C. Rahbek, Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* **480**, 516–519 (2011). pmid: [22089134](https://pubmed.ncbi.nlm.nih.gov/22089134/)
98. K. L. Laidre *et al.*, Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecol. Appl.* **18** (suppl.), S97–S125 (2008). doi: [10.1890/06-0546.1](https://doi.org/10.1890/06-0546.1); pmid: [18494365](https://pubmed.ncbi.nlm.nih.gov/18494365/)
99. P. Convey, in *Antarctic Peninsula Climate Variability: Historical and Paleoenvironmental Perspectives*, E. Domack *et al.*, Eds. (American Geophysical Union, Washington, DC, 2003), pp. 145–158.
100. J. Overpeck, C. Whitlock, B. Huntley, in *Paleoclimate, Global Change and the Future*, K. D. Alverson, R. S. Bradley, T. F. Pedersen, Eds. (Springer, Berlin, 2003), pp. 81–103.
101. R. B. Huey *et al.*, Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. Lond. B Biol. Sci.* **276**, 1939–1948 (2009). doi: [10.1098/rspb.2008.1957](https://doi.org/10.1098/rspb.2008.1957); pmid: [19324762](https://pubmed.ncbi.nlm.nih.gov/19324762/)
102. J. M. Sunday, A. E. Bates, N. K. Dulvy, Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. Lond. B Biol. Sci.* **278**, 1823–1830 (2011). doi: [10.1098/rspb.2010.1295](https://doi.org/10.1098/rspb.2010.1295); pmid: [21106582](https://pubmed.ncbi.nlm.nih.gov/21106582/)
103. A. A. Hoffmann, S. L. Chown, S. Cusella-Trullas, Upper thermal limits in terrestrial ectotherms: How constrained are they? *Funct. Ecol.* **27**, 934–949 (2013). doi: [10.1111/j.1365-2435.2012.02036.x](https://doi.org/10.1111/j.1365-2435.2012.02036.x)
104. M. B. Araújo *et al.*, Heat freezes niche evolution. *Ecol. Lett.* **16**, 1206–1219 (2013). doi: [10.1111/ele.12155](https://doi.org/10.1111/ele.12155); pmid: [23869696](https://pubmed.ncbi.nlm.nih.gov/23869696/)
105. R. K. Colwell, G. Brehm, C. L. Cardelus, A. C. Gilman, J. T. Longino, Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**, 258–261 (2008). doi: [10.1126/science.1162547](https://doi.org/10.1126/science.1162547); pmid: [18845754](https://pubmed.ncbi.nlm.nih.gov/18845754/)
106. L. Gilsson, T. P. Dawson, S. Jack, M. A. McGeoch, Accommodating climate change contingencies in conservation strategy. *Trends Ecol. Evol.* **28**, 135–142 (2013). doi: [10.1016/j.tree.2012.10.008](https://doi.org/10.1016/j.tree.2012.10.008); pmid: [23146578](https://pubmed.ncbi.nlm.nih.gov/23146578/)
107. W. B. Foden *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). doi: [10.1371/journal.pone.0065427](https://doi.org/10.1371/journal.pone.0065427); pmid: [23950785](https://pubmed.ncbi.nlm.nih.gov/23950785/)
108. L. P. Shoo *et al.*, Engineering a future for amphibians under climate change. *J. Appl. Ecol.* **48**, 487–492 (2011). doi: [10.1111/j.1365-2664.2010.01942.x](https://doi.org/10.1111/j.1365-2664.2010.01942.x)
109. P. Williams *et al.*, Planning for climate change: Identifying minimum-dispersal corridors for the Cape

- Proteaceae. *Conserv. Biol.* **19**, 1063–1074 (2005). doi: [10.1111/j.1523-1739.2005.00080.x](https://doi.org/10.1111/j.1523-1739.2005.00080.x)
110. R. Altwegg *et al.*, Novel methods reveal shifts in migration phenology of barn swallows in South Africa. *Proc. R. Soc. Lond. B Biol. Sci.* **279**, 1485–1490 (2012). doi: [10.1098/rspb.2011.1897](https://doi.org/10.1098/rspb.2011.1897); pmid: [22072608](https://pubmed.ncbi.nlm.nih.gov/22072608/)
111. N. E. Zimmermann *et al.*, Climatic extremes improve predictions of spatial patterns of tree species. *Proc. Natl. Acad. Sci. U.S.A.* **106** (suppl. 2), 19723–19728 (2009). doi: [10.1073/pnas.0901643106](https://doi.org/10.1073/pnas.0901643106); pmid: [19897732](https://pubmed.ncbi.nlm.nih.gov/19897732/)
112. M. V. Lomolino, in *Frontiers of Biogeography: New directions in the geography of nature*, M. V. Lomolino, L. R. Heaney, Eds. (Sinauer, Sunderland, MA, 2004), pp. 293–296.
113. K. J. Feeley, M. R. Silman, The data void in modeling current and future distributions of tropical species. *Glob. Change Biol.* **17**, 626–630 (2011). doi: [10.1111/j.1365-2486.2010.02239.x](https://doi.org/10.1111/j.1365-2486.2010.02239.x)
114. A. Felton *et al.*, Climate change, conservation and management: An assessment of the peer-reviewed scientific journal literature. *Biodivers. Conserv.* **18**, 2243–2253 (2009). doi: [10.1007/s10531-009-9652-0](https://doi.org/10.1007/s10531-009-9652-0)
115. B. R. Scheffers, L. N. Joppa, S. L. Pimm, W. F. Laurance, What we know and don't know about Earth's missing biodiversity. *Trends Ecol. Evol.* **27**, 501–510 (2012). doi: [10.1016/j.tree.2012.05.008](https://doi.org/10.1016/j.tree.2012.05.008); pmid: [22784409](https://pubmed.ncbi.nlm.nih.gov/22784409/)
116. D. Nogués-Bravo, M. B. Araújo, M. P. Errea, J. P. Martínez-Rica, Exposure of global mountain systems to climate warming during the 21st Century. *Glob. Environ. Change* **17**, 420–428 (2007). doi: [10.1016/j.gloenvcha.2006.11.007](https://doi.org/10.1016/j.gloenvcha.2006.11.007)
117. R. W. Katz, G. S. Brush, M. B. Parlange, Statistics of extremes: Modeling ecological disturbances. *Ecology* **86**, 1124–1134 (2005). doi: [10.1890/04-0606](https://doi.org/10.1890/04-0606)
118. K. Fraedrich, F. W. Gerstengarbe, P. C. Werner, Climate shifts during the last century. *Clim. Change* **50**, 405–417 (2001). doi: [10.1023/A:1010699428863](https://doi.org/10.1023/A:1010699428863)
119. W. W. Hargrove, F. M. Hoffman, Potential of multivariate quantitative methods for delineation and visualization of ecoregions. *Environ. Manage.* **34** (suppl. 1), S39–S60 (2004). doi: [10.1007/s00267-003-1084-0](https://doi.org/10.1007/s00267-003-1084-0); pmid: [15883870](https://pubmed.ncbi.nlm.nih.gov/15883870/)
120. Materials and Methods are available as supplementary materials on Science Online.

Acknowledgments: We thank H. Prasad for assisting with baseline climate data handling and B. Sandel for sharing the R script for the spatial gradient of climate change. We

are grateful to three anonymous reviewers for constructive comments on our manuscript. R.A.G. is funded through a Foundation for Science and Technology (FCT) Ph.D. studentship (SFRH/BD/65615/2009), M.B.A. through the FCT PTDC/AAC-AMB/98163/2008 project and the Integrated Program of IC&DT Call N° 1/SAESCTN/ALENT-07-0224-FEDER-00175, and M.C. through the Academy of Finland (grant 257686). C.R., R.A.G., and M.B.A. thank the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate, and C.R. and M.B.A. also thank the Imperial College London's Grand Challenges in Ecosystems and Environment initiative for support of their research.

Supplementary Materials

www.sciencemag.org/content/344/6183/1247579/suppl/DC1
Materials and Methods
Figs. S1 to S7
Tables S1 and S2
References ([121–165](#))

[10.1126/science.1247579](https://doi.org/10.1126/science.1247579)