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Science **332**, 53 (2011);
DOI: 10.1126/science.1200303

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Beyond Predictions: Biodiversity Conservation in a Changing Climate

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Climate change is predicted to become a major threat to biodiversity in the 21st century, but accurate predictions and effective solutions have proved difficult to formulate. Alarming predictions have come from a rather narrow methodological base, but a new, integrated science of climate-change biodiversity assessment is emerging, based on multiple sources and approaches. Drawing on evidence from paleoecological observations, recent phenological and microevolutionary responses, experiments, and computational models, we review the insights that different approaches bring to anticipating and managing the biodiversity consequences of climate change, including the extent of species' natural resilience. We introduce a framework that uses information from different sources to identify vulnerability and to support the design of conservation responses. Although much of the information reviewed is on species, our framework and conclusions are also applicable to ecosystems, habitats, ecological communities, and genetic diversity, whether terrestrial, marine, or fresh water.

Alarming predictions about the potential effects of future climate change are prompting policy responses at local to global levels (1, 2). Because greenhouse gas emissions to date commit Earth to substantial climate change in the coming decades (3), the potential for loss of biodiversity, termination of evolutionary potential, and disruption of ecological services must be taken seriously. Averting deleterious consequences for biodiversity will require immediate action, as well as strategic conservation planning for the coming years and decades. But how good are our current predictions, and how fit are they for conservation planning purposes?

To date, assessments of climate-change impacts on biodiversity have largely been based on empirical niche (or climate-envelope) models (4). For most species, these models indicate large geographic displacements and widespread extinctions. However, niche models are best suited to identifying exposure to climate change, which is only one aspect of vulnerability. Assessing biodiversity consequences of climate change is a multifaceted problem, requiring consideration of all aspects of vulnerability: exposure, sensitivity, and adaptive capacity (5) (see Box 1). Additional sources of evidence include observations of responses to climate changes (both past and present),

experiments, and mechanistic (process) modeling based on ecophysiology and population biology. These studies show a range of natural coping mechanisms among populations exposed to climate change, with diverse consequences for resilience at local to global scales. The capacity to cope depends on both intrinsic factors (species biology, genetic diversity) and extrinsic factors (rate, magnitude, and nature of climatic change). Integration of multiple approaches and perspectives is needed for more accurate information about which species and habitats, in which places, are likely to be most at risk, as well as how conservation managers can leverage adaptive capacities in natural systems to maximum advantage. There is a wealth of knowledge upon which to draw.

How Reliable Is the Current Generation of Predictions?

Climate-change impacts on biodiversity, both positive and negative, are already manifest in recent widespread shifts in species ranges and phenological responses (6, 7). Although human land use remains the main driver of present-day species extinction and habitat loss (8), climate change is projected to become equally or more important in the coming decades (9, 10). Assessing the biodiversity consequences of climate change is complicated by uncertainties about the degree, rate, and nature of projected climate change (11), the likelihood of novel and disappearing climates (12), the diversity of individual-species responses to a broad suite of interacting climate variables (6), and interactions of climate-change effects with other biotic factors (e.g., competition, trophic relationships) and stressors (land use, invasive species, pathogens, pollutants) (13, 14).

Syntheses of climate change and biodiversity for decision-makers, conservation organizations, and governments (1, 2, 15) have relied heavily on empirical niche (or climate-envelope) modeling and analog scenarios of climate space (4). This approach uses statistical relationships between current climate variables and geographic patterns of species distribution and/or abundance to define an "environmental space" associated with a particular species. The models are then applied to climate projections from general circulation models (GCMs), yielding maps of species ranges predicted under future climate scenarios. Application of these models has led to dire warnings of biodiversity loss (16). This has led in turn to calls for radical and immediate intervention measures, including the redesign of protected-area systems, development of new areas for restoration and management, and human-assisted migration (17, 18).

Box 1. Vulnerability in the context of climate and biodiversity.

Vulnerability is the extent to which a species or population is threatened with decline, reduced fitness, genetic loss, or extinction owing to climate change. Vulnerability has three components: exposure (which is positively related to vulnerability), sensitivity (positively related), and adaptive capacity (negatively related).

Exposure refers to the extent of climate change likely to be experienced by a species or locale. Exposure depends on the rate and magnitude of climate change (temperature, precipitation, sea level rise, flood frequency, and other hazards) in habitats and regions occupied by the species. Most assessments of future exposure to climate change are based on scenario projections from GCMs often downscaled with regional models and applied in niche models.

Sensitivity is the degree to which the survival, persistence, fitness, performance, or regeneration of a species or population is dependent on the prevailing climate, particularly on climate variables that are likely to undergo change in the near future. More sensitive species are likely to show greater reductions in survival or fecundity with smaller changes to climate variables. Sensitivity depends on a variety of factors, including ecophysiology, life history, and microhabitat preferences. These can be assessed by empirical, observational, and modeling studies.

Adaptive capacity refers to the capacity of a species or constituent populations to cope with climate change by persisting in situ, by shifting to more suitable local microhabitats, or by migrating to more suitable regions. Adaptive capacity depends on a variety of intrinsic factors, including phenotypic plasticity, genetic diversity, evolutionary rates, life history traits, and dispersal and colonization ability. Like sensitivity, these can be assessed by empirical, observational, and modeling studies.

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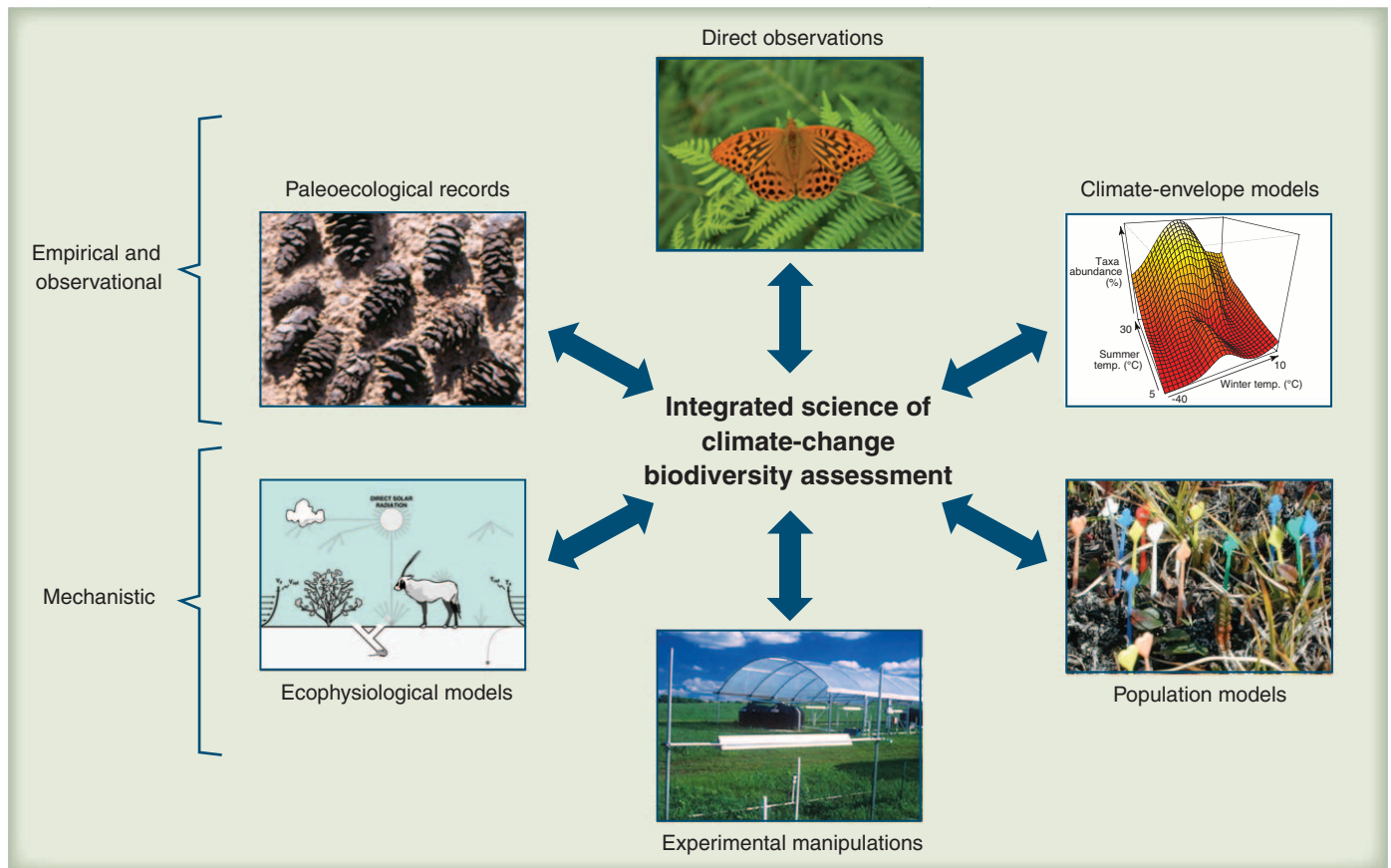


Fig. 1. An integrated science of climate-change biodiversity assessment will draw from multiple sources and approaches. Each provides useful but incomplete information on exposure, sensitivity, and adaptive capacity. Integration of these approaches will provide a more robust basis for vulnerability assessment and allocation of resources for conservation and adaptation. Direct observations, including long-term monitoring, are applicable at a broad range of scales and can be used to assess all aspects of vulnerability. Paleoecological records extend the observational foundation to encompass a broader range of rates, magnitudes, and kinds of climate change. They can reveal adaptive capacity and risks. Climate-envelope (or niche) models are statistical models based on correlations

between geographic patterns of species distributions and climate, and are best suited for assessment of exposure. Mechanistic models such as population models and ecophysiological models are diverse, require taxon-specific parameters, and are often coupled. They are particularly effective in assessing sensitivity and adaptive capacity. Experimental manipulations provide information on sensitivity and adaptive capacity, and are valuable in parameterizing mechanistic models. [Photo credits: direct observations (silverwashed fritillary, *Argynnis paphia*), www.learnaboutbutterflies.com; climate-envelope models, S. Brewer; population models, S. T. Jackson; experimental manipulations, A. K. Knapp; ecophysiological models, W. P. Porter; paleoecological records, S. T. Jackson]

The heavy reliance of conservation management and policy on a single scientific approach creates risks of policy or management failures, particularly given that the underlying assumptions of that approach are under debate. Critiques center on the correlative nature of the niche models, scale dependency, the difficulty of reliable extrapolation outside observed climate space, and failure to represent key ecological and evolutionary processes that could allow species to persist in a heterogeneous landscape (13, 19–23). Niche models impart ease of use and power in explaining modern distributions (24), but their efficacy in assessing extinction risk, delineating suitable future habitats, and predicting ecological outcomes is unproven (25).

Niche models provide a tool for assessing exposure to climate change as projected in various GCM scenarios (Box 1). Given the global nature of projected climate changes (1), exposure is inevitable for any species that has a finite geographic distribution, although the amount of

climate change to be faced varies widely among species. However, exposure is only one of many factors determining the impacts of climate change. Assessment of vulnerability must also include climate sensitivity and adaptive capacity (5) (Box 1).

Complementary methodologies are available that tell us much more about natural responses to climate change (Fig. 1). These indicate that biodiversity losses may not be as large as predicted from niche models, although the rate of change and land use (habitat loss or destruction, harvesting) remain barriers to some natural response mechanisms. Approaches based on observations in the present and the past, experiments, and new modeling techniques are developing rapidly. Integration of these approaches should provide the foundation for a robust science of climate-change assessment.

Elements of Integrated Climate-Change Assessment for Biodiversity

Ecological observations in real time. Many species are altering their geographic ranges and

adjusting phenological responses in ways consistent with the relatively small climate changes of the past few decades (6, 26). Although some species are undergoing rapid, widespread population declines, in most cases the primary drivers of decline involve land-use change and habitat fragmentation, biotic interactions, pathogens, and invasive species (8, 9). To date, there is more evidence for climate-driven range expansion than for range contraction (27). It might appear that many species are coping with climate change. However, range contraction and population extirpation (local extinction) may be more difficult to document than expansion and migration, owing to undersampling of small or isolated populations, long-term local persistence of populations, and extinction lags (28). Extirpations already entrained by climate change may take years or decades to run their full course (29). Detecting (or forecasting) species decline is challenging because the processes are not well understood, and species decline as well as loss

of ecosystem function may involve threshold transitions (30–32).

New knowledge emerges from real-time tracking of species responses to climate change, but direct observations are not, on their own, a sufficient method for forecasting risks or the intrinsic capacity of species and populations to adapt. It remains unknown whether the ongoing range expansions and phenological shifts will allow species populations to survive, or whether these are transient responses in populations with reduced fitness in the changed environment. Future

environments will display novel combinations of climate variables (12). So far there is limited evidence of microevolutionary adaptive change (33), perhaps because reliable methods to detect microevolution have rarely been applied (34, 35). Furthermore, recent case studies where the causal processes driving population responses to climate change have been disentangled suggest that the climate variables, and the way they interact with species life history, can be both complex and context-specific (30, 31, 36–38). The use of observational evidence will therefore need to be

applied alongside deeper understanding of the biological differences among species that determine their fate under climate change.

Intrinsic adaptive capacity for climate change. Observations, experiments, and mechanistic models indicate that many species populations have the capacity to adjust to climate change in situ via phenotypic plasticity (e.g., acclimation, acclimatization, developmental adjustments) (Fig. 2) (35, 39) and microevolution (40, 41), and that many populations are able to disperse locally to suitable microhabitats (42, 43) or regionally to

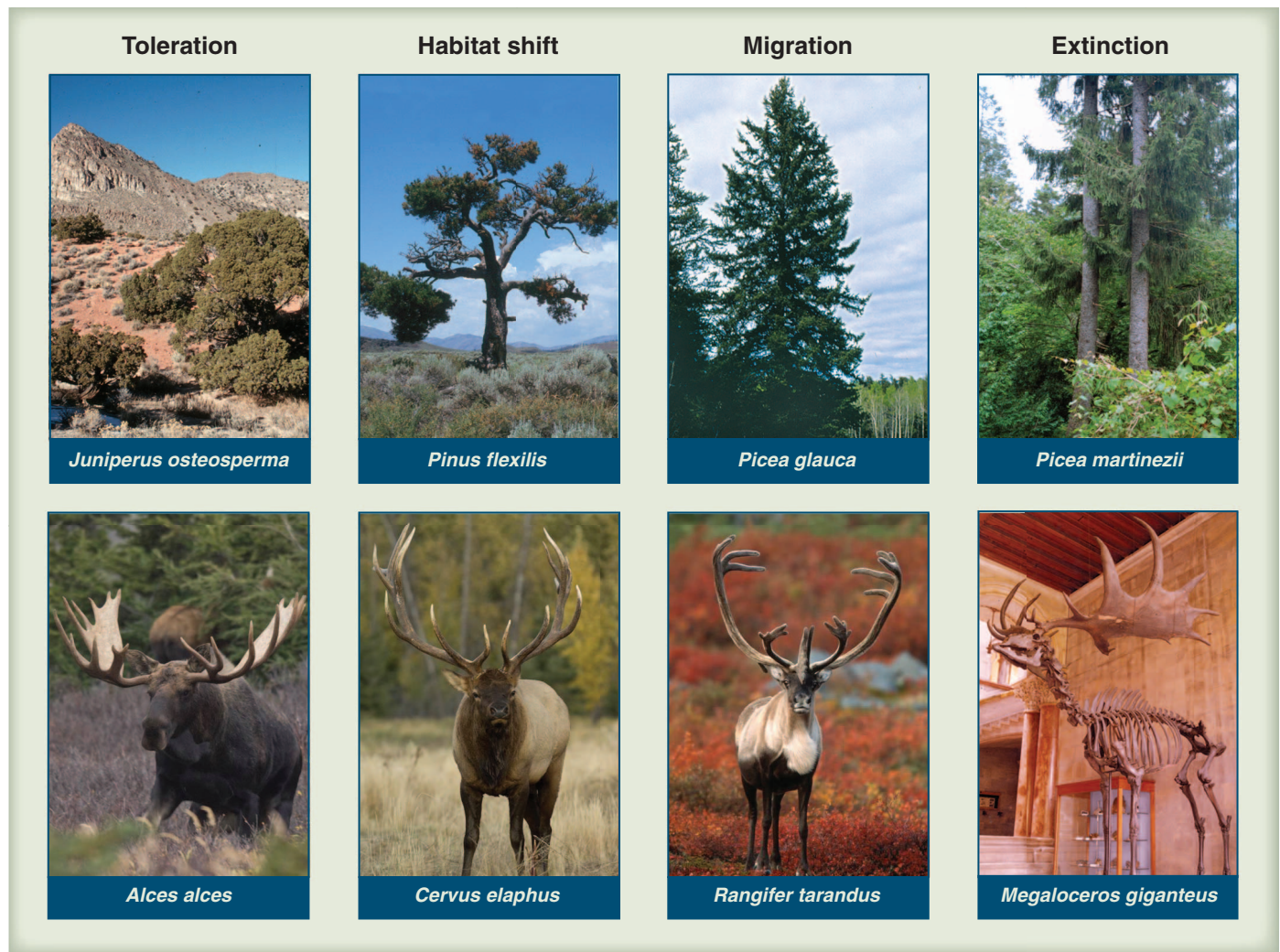


Fig. 2. Representative modes of population and species-range response to environmental changes since the last glacial maximum, documented for selected North American conifer trees and Eurasian cervids. Populations of many species have persisted in situ at individual sites since the last glacial maximum (toleration) 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. Both migration and habitat shift are forms of environment tracking, in which species adjust their geographic locations to track suitable environments. 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 multiple

modes. 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). *Alces alces* has also undergone a severe genetic bottleneck. Differences among modes within and among species depend on rates, magnitudes, and geographic patterns of climatic change, the capacity of species populations to adapt (via phenotypic plasticity, evolution, and/or dispersal), and other factors (e.g., geographic barriers, and other stressors and interactions). References, additional examples, and detailed discussion are provided in the supporting online material. [Photo credits: S. T. Jackson (*Juniperus osteosperma*, *Pinus flexilis*, *Picea glauca*, *Picea martinezii*); A. D. Barnosky (*Megaloceros giganteus*); www.grambophoto.com (*Alces alces*, *Cervus elaphus*, *Rangifer tarandus*)]

newly suitable locales (44). Each of these adaptive mechanisms has constraints, which may limit the capacity of species and populations to keep pace with high rates and magnitudes of climate change (35). These processes are, however, the subject of an extensive ecological and evolutionary literature, which has so far been underexploited for determining adaptive capacity.

Given the number and diversity of species potentially under threat, the synthesis and application of existing evidence on adaptation will provide necessary—but not sufficient—information on adaptive mechanisms and capacities. The environmental controls and absolute limits of phenotypic plasticity, and the environmental dependence of optimum phenotypes (45), must be determined empirically for a range of species to predict in situ ecological and evolutionary responses to environmental change (34, 35). Empirical and theoretical studies of relevant ecological processes (propagule dispersal, establishment, population growth, fecundity, mortality, metapopulation dynamics) provide a basis for assessing response times for local, regional, and continental adjustments in distribution and abundance (46). This task can be simplified by using existing data and targeted studies of a range of representative taxa with diverse life history patterns and functional traits.

Biodiversity consequences of past climate changes. Increasingly, geohistorical records and paleoecological studies are being integrated with independent paleoclimate records to reveal effects of past climate changes (47, 48), which, in some periods and regions, were as large and rapid as those projected for the future (49, 50). Although possible future climates will be unlike those of the past, paleoecological records offer vital information about how species responded to different rates and degrees of change, with numerous case studies in terrestrial, freshwater, and marine ecosystems. The diverse outcomes for different taxa and life history types emphasize the range of past responses that are likely to be reflected in the present and future (Fig. 2).

Paleoecological observations can be further integrated with modern genetic and ancient DNA studies to assess the genetic consequences of these dynamics (47, 51–53). By determining past climate-driven losses in genetic and species diversity at local to regional scales, and by identifying the circumstances under which species have escaped extinction and populations have resisted extirpation, these studies can contribute to assessments of adaptive capacity and vulnerability (Fig. 2).

All species or species groups living on Earth today have persisted through a glacial-to-interglacial transition 20,000 to 12,000 years ago that included rapid, high-magnitude climate changes at all latitudes and in both terrestrial and marine environments. This transition followed immediately upon a series of abrupt, high-magnitude glacial-age climate changes with near-global impact (50). The last glacial-interglacial

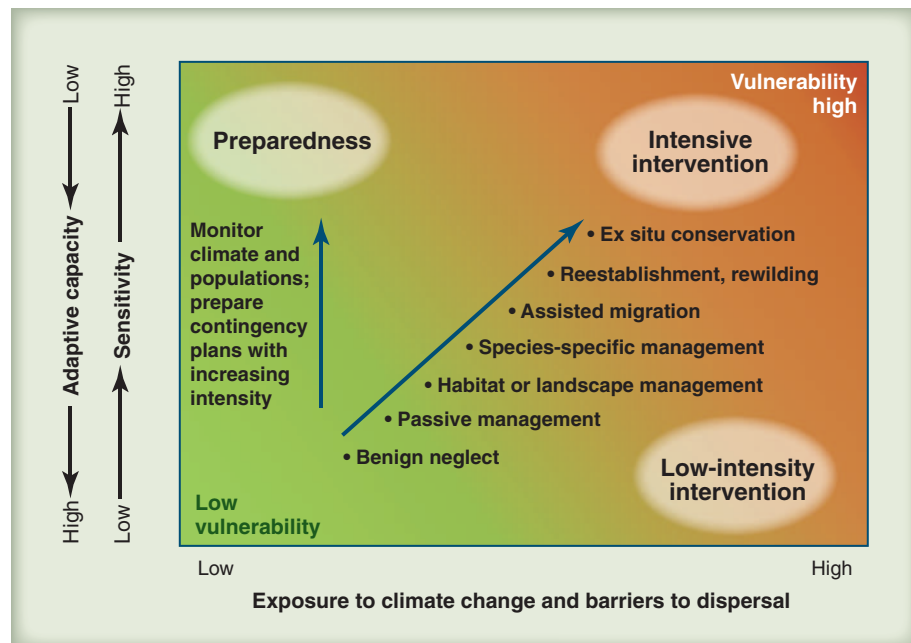


Fig. 3. The vulnerability of a species or ecosystem is based on its exposure to climate change, its sensitivity, and its inherent capacity to adapt to change. The relative balance of these different components of vulnerability would lead to different management interventions. The x axis represents the degree of exposure to climate change faced by species and communities (exogenous factors). This axis is largely determined by the species' or population's geographical location, the rate and magnitude of climate change anticipated for that region, and the size, cohesiveness, and connectivity of the species' habitat within and beyond that region. The other two measures from the vulnerability framework, adaptive capacity and sensitivity (see Box 1), are plotted together on the y axis. This axis is primarily determined by biological characteristics of species that influence their mobility, specificity, and sensitivity (endogenous factors). These include, for example, physiological constraints, phenotypic plasticity, evolutionary potential, dispersal and growth capacity, and biotic interactions critical to persistence. The relative position of species and ecosystems along the axes can inform decisions on appropriate research, monitoring, and management strategies. Decisions are also likely to be affected by costs and assessments of benefits (e.g., an ecosystem service value or lower cost might shift strategies implemented toward the top right). Circled text denotes generic conservation responses. Specific conservation responses that will be appropriate under the different circumstances are discussed in the text. Species in the upper left corner have high sensitivity to climate change but are expected to face relatively minor challenges. Such species are not a priority for intervention unless there is a change in climate-change pressures or landscape permeability. Their potential vulnerability means that they need to be monitored to ensure that they are thriving and remain unthreatened, with contingency plans that can be deployed in a timely manner in case of change. Species with high exposure but low sensitivity and high adaptive capacity (lower right corner) can presumably cope with change, and therefore need only low-intensity intervention as change becomes more extreme. Species in the upper right corner will have relatively high levels of both exposure and sensitivity; with decreasing adaptability, more intensive and specific management will be required.

cycle is only the most recent of at least 20 such cycles during the past 2 million years. Ecological and biogeographic responses to these climatic changes are particularly well documented for the past 10,000 to 20,000 years for many regions; such responses included repeated reorganization of terrestrial communities, changes in both the location and overall size of geographic ranges, and often rapid increases and decreases in sizes of local and regional populations (12, 49, 54–56).

The fact that the biodiversity on Earth today passed through these events indicates natural resilience and adaptive responses. Plant and animal species have shown capacity for persistence in small populations and microhabitats (52, 55, 57, 58),

long-distance migration and dispersal (59, 60), shifts along habitat gradients and mosaics (49, 61), and rapid expansion under favorable conditions (21). Many species have also undergone rapid range contraction and widespread population decline (16, 49, 62). Low genetic diversity indicates that many species have passed through recent genetic bottlenecks (63, 64). But few documented species extinctions can be ascribed solely to climatic change (65–67). Megafaunal extinctions occurred in North America at a time of rapid climate change during the last deglaciation, but human exploitation is also a possible cause (66). Extinction of only one plant species (*Picea critchfieldii*) has been documented during the last deglaciation (65).

Developing an Integrated Science of Climate-Change Biodiversity Assessment

The diverse sources of evidence discussed above can be integrated in a vulnerability framework (68). Vulnerability assessment has been suggested for prioritizing species at risk from climate change (5) and has been applied to both taxonomic and regional species groups (69, 70). The empirical foundation for trait-based climate-change vulnerability analysis is now starting to appear, including species that were exposed to relatively rapid climate shifts during the Quaternary (47, 71) as well as some recent studies (44, 72–75). A combination of expert opinion and expectations from ecological and evolutionary theory has been used to identify vulnerable traits for some groups (69, 76), including, for example, ecological specialists at higher trophic levels, with long generation times, poor dispersal ability, and low reproductive output. Body mass is strongly correlated with extinction risk and is often associated with other risk-promoting traits (e.g., delayed reproductive maturity, small geographic range) (77). Large range sizes may imply a large population size and can act to buffer against habitat loss or fragmentation. A broad geographical distribution may not only protect against individual habitat patches becoming climatically unsuitable, but may also foster high genetic variability. However, there are many exceptions to these generalizations, and paleoecological records suggest that they may break down under rapid climate change (49, 65).

Today, many species will be required to disperse rapidly through highly fragmented, human-dominated landscapes in order to keep pace with changing climate. Paleoecological evidence suggests that many plant species have responded to past rapid climate changes with migration rates orders of magnitude higher than predicted by mean observed dispersal distances. This suggests a potential role for rare long-distance dispersal (LDD) through the transportation of seeds in atmospheric updrafts and water courses, oceanic currents, and dispersal by birds and animals. Humans are very effective as LDD vectors and, like natural LDD mechanisms, do not require contiguous habitat to establish or maintain connectivity between populations, perhaps facilitating conservation strategies.

Given the evidence that the responses of species and communities to climate change will be highly variable, we need to move beyond predictions of future range changes, which may overestimate or underestimate risks in particular cases. Because of the variety of vulnerabilities and the factors that contribute to them, a one-size-fits-all strategy risks failure. We advocate a combination of strategies governed by assessment of vulnerability and its three components—exposure, sensitivity, and adaptive capacity—drawn from multiple lines of evidence.

Figure 3 displays species responses to climate change on two axes, based on a vulnerability framework. This approach can inform managers

about the relative urgency and the type of conservation action necessary. The diagonal axis in Fig. 3 broadly reflects increasing intensity of conservation interventions. This axis runs from “laissez-faire” (i.e., let natural processes run their course) to direct, targeted, and often intensive “command and control” interventions. The most adaptable and/or insensitive species and those with low exposure will need minimal interventions with low-level monitoring, a strategy we call “benign neglect.” For example, in the United States and Africa, vast territories designated as wilderness areas or reserves are “managed” with a laissez-faire approach. Active management is restricted to sporadic rewilding (e.g., top-predator reintroduction), low-impact eradication of invasive species, and removal of individuals dangerous to humans (e.g., rogue grizzly bears). These designations may, of course, change in the future. For example, it is likely that some ecosystems that currently receive minimal management, such as boreal forests, may require more active management under climate change.

As exposure and sensitivity increase and autonomous-response capability decreases, substantial benefits may result from simply designating new protected areas and undertaking low-level habitat management to reinforce species’ intrinsic dispersal and migration mechanisms. Analyses based on niche models have prescribed this approach (15). Periodic reevaluation of ongoing and planned protected-areas strategies may be needed to maintain potential for species resilience and mobility under climate change. For example, dynamic placing of buffer zones, removal of barriers, and establishment of corridors or “stepping stones” within a wider landscape may be necessary (78), although the definition, costs, and benefits of connectivity are under debate (79). A complementary strategy is to maintain high within-region habitat heterogeneity (edaphic, topographic, or elevational), which provides more options for both natural populations and conservation managers (80).

In any habitat or community, some species may require specific actions for their conservation or to retain critical biological interactions. Intermediate strategies—including intervention to arrest or divert natural succession or ecosystem regime shifts, maintenance of specific habitats or habitat diversity, and targeted interventions to restore disrupted species interactions (e.g., pollinator or plant-herbivore networks)—are now widely used. Species-specific management may be costly and intensive, but it can reverse the fate of endangered species (8).

Intensive intervention strategies include assisted migration and translocation of species outside their native range (18). Reestablishment and rewilding involve intensive habitat management to restore critical habitat types, with whole communities recreated from populations surviving elsewhere. These are generally considered to be high-risk strategies because of potentially negative ecological, evolutionary, and economic im-

pacts (81) and ethical concerns (82). Despite these risks, such interventions may be necessary in some circumstances. It is not too early to debate whether, when, and how such strategies should be deployed (83). Finally, controlled ex situ conservation, involving captive breeding and genetic manipulation in zoological and botanical gardens and recently developed cryogenic seed banks, may contribute to conserving species or populations with a view to future release or reintroduction.

The particular strategies deployed will depend on the circumstances of the species (Fig. 3) and will also vary in the financial and other resources they require. The perceived conservation value of particular habitats and species will also play a part and may be informed by ecosystem service assessments. Thus, management decisions will depend on judgments of potential risks and benefits balanced against costs and available or anticipated resources. Decisions must balance tradeoffs. For example, creating permeable landscapes to facilitate migration may be more effective under climate change than intensive management in “static” conservation areas as climate change proceeds, but may risk further spread of disease or invasive species. This assessment should aim to maximize the likelihood of the desired management outcome, minimize the financial costs, and assess associated risks.

Outlook

Conservationists are increasingly concerned about biodiversity disruption and loss as climate-change impacts intensify in the coming decades. So far the focus has mostly been on multispecies, place-based predictions with emphasis on exposure to climate change. Our review of the evidence from paleohistory, current observations, experiments, and models emphasizes the extent to which species vary in their vulnerability. This variation represents perhaps our best hope for maintaining biodiversity and its associated ecological goods and services in the future. Developing effective strategies will rely on improved understanding of the nature of the climate threat to species, and the way that it interacts with their natural coping mechanisms. The rich history of ecological, evolutionary, and paleontological field studies, brought together with relevant climate data and with appropriate evolutionary and ecological theory and modeling, has the potential to transform the way that we assess climate-change vulnerability. More appropriate conservation actions will result from taking into account all three aspects of vulnerability—species sensitivity, adaptive capacity, and exposure.

Many orthodox conservation practices, such as the restoration and protection of habitats and the removal of anthropogenic pressures unrelated to climate, will continue to increase species and ecosystem adaptive capacity to climate change. Additional, more informed approaches will require new research, especially to identify and parameterize key ecological and evolutionary

variables, and to develop models that are capable of providing reliable predictions without being unrealistically data-hungry. The evidence is there to build upon. Now is the time for conservation biology to move beyond predictions to analysis, diagnosis, and design and implementation of effective measures to protect biodiversity.

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- We thank three anonymous reviewers for helpful comments. Some of the ideas presented here emerged from discussions among the participants at the NERC QUEST (Quantifying and Understanding the Earth System) Working Group on Biodiversity and Climate Change, which was cosponsored by and held at the Royal Botanic Gardens, Kew, in September 2009. Supported by QUEST (J.I.H. and I.C.P.), NSF grant 0949308 (S.T.J.), and the UK Natural Environment Research Council (G.M.M.).

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10.1126/science.1200303

ERRATUM

Post date 1 April 2011

Review: "Beyond predictions: Biodiversity conservation in a changing climate" by T. P. Dawson *et al.* (1 April, p. 53). When originally published, Fig. 2 was incorrect due to an editorial error. The third column in Fig. 2 was mislabeled as "Habitat shift." The PDF and HTML versions were corrected on the day of publication. This PDF contains the corrected figure.