



The Future of Species Under Climate Change: Resilience or Decline? Craig Moritz and Rosa Agudo *Science* **341**, 504 (2013); DOI: 10.1126/science.1237190

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

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REVIEW

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

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

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

What Theory Says: Concepts and Predictive Models

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

Exposure is typically measured as shifts in mean precipitation or temperature at the mesoscale (e.g., 1 to 100 km²). For temperature, ensemble forecasts tend to predict the largest increases in northern high latitudes and the lowest across Downloaded from www.sciencemag.org on August 6, 2013

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

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

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

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Fig. 1. Global mean temperate fluctuations and scales of inference across the historical record and future predictions. The paleoclimate record is modified from http://commons.wikimedia.org/wiki/File:All_palaeotemps. png, data for the 20th-century record were obtained from http://data.giss. nasa.gov/gistemp/graphs_v3/, and forecasts of future change are adapted

climatic conditions. Species that actively thermoregulate may be able to select microhabitats that are buffered from extreme conditions (20, 37), though this can also restrict activity, which may lead to local extinction (38). This aspect of response to climate change has not been studied sufficiently and warrants greater attention. Dispersal to track geographic shifts in climate is clearly the dominant response measured from paleontological and 20th-century records (see below). The scale of dispersal required is a function of both the regional magnitude of climate change and topography, combined with the species sensitivity (23).

Predicted Impacts of Future Climate Change

Forecasts of potential species responses to future climate change come in two varieties: (i) correlative or mechanistic models of individual species (39) or (ii) prediction of higher-level properties such as species richness (3) or turnover (40). Correlative models are currently the most widespread and scalable method (41), but they have inherent limits. These models typically apply some form of climate envelope approach, assessing whether the (realized) climate niche occupied by a species continues to exist within the current geographic range and whether it will shift elsewhere or cease to exist. This approach has often been criticized for lacking a direct mechanistic basis and the inherent danger of extrapolation (9). Additionally, these models are generally computed at a coarse spatial resolution and fail to capture spatial variability in temperature over

from (107), figure SPM.5 (different colors represent predictions under different models). Note the differences in scale on the *x* axis and that forecasts under higher-emission scenarios exceed the natural variability observed over the historical record. ΔT , change in temperature; Yrs BP, years before the present.



Fig. 2. Factors affecting species vulnerability to climate change. (A) Schematic of the pathway from exposure to broad-scale climate change to species vulnerability [see (1, 2) for analogous representations]. (B) Limits to evolutionary rescue imposed by trait heritability, the intrinsic rate of population growth, and the rate of change in the environment (e.g., temperature). This schematic is modified from (36) and is based on theoretical models in (29).

tens to hundreds of meters, at which the buffering role of microhabitat heterogeneity may be crucial for species persistence (18, 42). Thus, correlative models are probably a better measure of exposure than of species vulnerability to climate change.

The actual predictions of effects on species persistence are often dire, however. For example, one prominent analysis predicted that 15 to 37% of species would be endangered or extinct by 2050 (*3*). Another predicts more than a 50% loss of climatic range by 2080 for some 57% of widespread species of plants and 34% of animals (*4*). Montane taxa are expected to lose range area

as they shift upward with warming. Again, predicted effects are catastrophic (43-45) and could be even worse for the highly endemic biotas of tropical montane forests if the cloud base lifts (46). For the tropical lowlands, high levels of species attrition are predicted because of narrower physiological tolerances (47) and a high velocity of change due to shallow temperature gradients (48). Reduction of species ranges is expected to result in substantial loss of geographically structured genetic variation, perhaps including cryptic taxa (49, 50). Yet, we must acknowledge the level of uncertainty of these predictions and the possibility that these



models are overestimating extinction risk. Future models should be improved by incorporating key parameters such as finer-scale topographic heterogeneity (18), interaction of biotic (51, 52) and other anthropogenic factors (7, 45, 53), species physiological constraints and plastic acclimation capacity (39), as well as demographic processes [see for instance, the recent findings of Reed *et al.* (54) in a wild population in which density-dependent compensation counteracts the reduced fledgling rates due to phenological mismatch provoked by climate change].

What the Data Say: Species Responses to Past Climate Change

The Paleoecological Record

The fossil record and the imprint of history in geographic patterns of DNA diversity (phylogeography) provide valuable insights into how species responded to past shifts in global temperature, including rapid warming events at the Pleistocene-Holocene transition (Fig. 1). These sources of information on historical responses have distinct limitations that can be partially overcome by combining types of evidence (see below). The fossil record varies in extent and resolution according to preservation conditions (55, 56); that is, a sparse faunal record for the tropics; underrepresentation of small, rare, and physically fragile species; and, sometimes, low taxonomic resolution (i.e., identification to genus rather than species). Phylogeographic analysis, on the other hand, affords higher spatial resolution but typically has low temporal precision compared with fossils.

The picture emerging from fossil evidence, including the Pleistocene-Holocene transition, is one of both robustness and dynamism. To simplify, there was no signal of elevated extinction through periods of rapid change (5, 6, 57), and, at the level of genera, composition and trophic

structure of mammalian communities appear robust [(5), but see (58)]. One exception is recent megafaunal extinctions, where climate change and human impacts likely combined with devastating consequences (59, 60). This is not to say that the biota was static through past climate change-far from it. The dominant response was idiosyncratic shifts in geographic range (61-63) with concomitant shuffling of community composition, often resulting in nonanalog assemblages (9). Geographic shifts are well described for mammals and appear more pronounced for habitat or dietary specialists than generalists (5, 64, 65). Another type of response described well in mammals through past warming periods is decrease in body size, a key ecological trait (5, 66).

Comparative phylogeographic studies, often combined with paleoclimatic modeling of geographic ranges, offer another window on past species responses (67) and can identify regions in which taxa persisted through past climate change; that is, evolutionary refugia (68-70). Again, such studies point to disparate species' responses, with some evidently persisting in many areas and others in just a few major refugia, despite a common history of climate change across the focal landscape (71-74). When combined with fossil evidence and spatial models, such studies highlight the extent of range shifts but also the importance of scattered microrefugia, which are important for range recovery (6, 75) and perhaps also harbor distinct adaptations (76, 77). Going further, direct DNA analyses of subfossils provide a much clearer picture of population dynamics through climate change (78) and, for megafauna, highlight differences among species in response to the twin challenges of climate change and human colonization (7, 79).

The 20th-Century Record

The discord between predictions of high extinction under future climate change and relatively high resilience through paleoclimatic change could be partly due to the limitations of the fossil record (see above) but may also reflect the fact that, with the possible exception of Holocene megafauna, species were previously able to respond in the absence of other human-caused impacts on natural systems. Thus, even though the rate of expected future change may be much faster than that over the past century, there is value in examining how species have responded to climate change over the 20th century.

There is abundant evidence for climaterelated changes in distributions and timing of life history events of species over the past decades. Meta-analyses across thousands of species report strong trends in shifts of geographic range limits, predominantly toward higher latitudes and higher elevations for terrestrial taxa and lower depths for marine taxa, as expected in a warming world (80-82). These trends are reflected even in increasing representation of more tropical species in major fisheries (83). Recent climate change has also affected the communities' composition by increasing the dominance of generalist taxa and larger basal prey species, whereas habitat specialists, rare species, and species with more northerly distributions have declined (84-87).

Yet again, a dominant feature is marked heterogeneity of species responses. For example, Chen *et al.* (80) report that about one-quarter of species moved downhill or toward lower latitudes, opposite of what was expected. This observation may reflect marked differences in 20th-century climate change across regions and between marine and terrestrial systems (88). However, the same is seen within a single biome [e.g., UK terrestrial species (80)]. To take one example, studies across strong environmental gradients in California revealed both upward and downward shifts in plants (89) and birds (90), whereas montane small mammals mostly shifted upward, in accord with increasing minimum temperatures and lead-





range shifts. Data are from (90, 91). (**B**) Decreased extent and increased fragmentation of the range of the alpine chipmunk (*Tamais alpinus*) across Yosemite, with a concomitant increase in genetic structure associated with the upward contraction of this montane specialist from the early 20th century to the present. Modified from (108).

ing to substantial range contractions (91) (Fig. 3). Yet even closely related species (e.g., different species of chipmunk, voles, or field mice) showed disparate responses. Lenoir et al. (92) summarize some of these examples and suggest habitat modification, as well as species interactions and their interplay with climate change, as possible mechanisms explaining the observed variability. These observations highlight the complexity of the process and the difficulty of accurately predicting future effects based on actual models. This points to the need for a more nuanced approach to predicting species vulnerability-one that also considers changes in precipitation, productivity, and habitat structure (89, 90). It is difficult to identify traits that predict whether or not species will track temperature change (93). Species expanding ranges upward or to higher latitudes tend to be weedy, prolific, and/or ecological generalists (86, 87, 91, 94). But as yet, few, if any, traits provide robust prediction of which species are observed to contract in range. It is the latter we should be most concerned about.

Shifts in phenology (e.g., earlier flowering, breeding, and migration and reduced migration) are also widely observed in the 20th-century record and could cause temporal mismatch between strongly interacting species, especially where these species employ different environmental cues (28, 95, 96). As expected with warming, decreasing body size has been observed in several studies of birds and mammals (97). This response seems to be plastic rather than genetic (98, 99), or it may be related to extended food availability rather than direct physiological effects (100). Again, idiosyncrasy is the trend; some hibernating mammals show increasing body size, perhaps due to a longer period of food availability (100, 101). Finally, as yet, no species extinctions are clearly attributable to climate change per se, although several studies recorded local extinctions and population declines (102). Nevertheless, it is very difficult to establish causative relationships between warming and population declines or extinction, due to the interaction with other anthropogenic factors such as habitat loss or previously unseen pathogens [e.g., declines of amphibians in the montane neotropics (103, 104)]. A recurring message is that we have insufficient knowledge of the proximate cause(s) of observed species declines under global warming: The few examples appear to be more closely related to indirect ecological effects than to demonstrable physiological challenges (102).

Management in the Face of Change and Uncertainty

The historical record over millennia and the past century demonstrates that species do respond to climate change, albeit in ways difficult to predict individually. As we move into climate conditions without recent parallel and across ecosystems already strongly affected by humans, the challenge is to increase resilience of natural systems now, in conjunction with continuing research to improve our capacity to predict vulnerability (1, 2). These priorities must undoubtedly be accompanied by the urgent mitigation of the main culprit, the greenhouse gas emissions (4).

What Do We Know?

The simplest and most strongly supported response of species is to shift geographically to track their climatic niche. Observed responses to paleoclimatic change emphasize the importance of refugia—both macro- and microrefugia (16)— as key landscapes to protect.

Given rapid climatic change, evolutionary rescue of intrinsically sensitive species is most plausible for those with short generation times and high potential population growth. In particular, for potentially sensitive species with long generation times, every effort should be made to minimize other stressors on population viability and to monitor population trends.

Taken together, managing and restoring ecoevolutionary dynamics across large ecologically heterogeneous landscapes, including long-term climatic refugia, and enabling habitat connections to these refugia are increasingly acknowledged as priorities. Recognizing that species and ecosystems are naturally dynamic and are likely to become more so with anthropogenic impacts, maintaining the status quo should not be the conservation goal; rather, we should seek to manage system dynamics within bounds to avoid largescale state changes (105, 106).

What Don't We Know? Some Research Priorities

Understanding and predicting the effects of future climate change on species, let alone communities and ecosystems, is an urgent and fundamental challenge to this generation of biologists. Although we have identified many areas of uncertainty and more can be found in the broader literature, we will now highlight just three areas of immediate relevance to conservation decision-makers.

First, understanding the capacity of species to buffer effects of climate change in situ is crucial if we are to predict and manage vulnerable species. Key aspects include better understanding of the limits of plasticity of key traits and microhabitat buffering. Along the same lines, aside from some generalizations, research on trait-based prediction of vulnerability has a long way to go before it can provide a robust management tool. Progress on these aspects will come from intensive analyses of the proximate causes of climate-related species decline, as well as further comparative studies.

Second, predictive models of spatial and demographic responses of species must be tested and improved, yet must also remain scalable to many species. Parameter-rich models incorporating demography, dispersal, intrinsic limits, and evolutionary response are ideal and can be applied to model systems. The identification of generalizations and hybrid approaches will enable

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more robust predictions for larger numbers of less well known species.

Third is the vexing problem of species interactions: Do tipping points exist and lead to irreversible state change (*52*, *105*)? How do we reconcile these concerns with evidence for dynamism of communities and resilience of trophic structure through past climate change?

Underpinning all of the above is the need to make greater use of the record of the responses to past climate change, over time scales from millennia to decades. The potential of museums and herbaria collections and records is becoming more apparent, but much more needs to be done to capture and apply the invaluable data and field notes from long-term studies of 20th-century ecologists.

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REVIEW

Climate Change Impacts on Global Food Security

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Climate change could potentially interrupt progress toward a world without hunger. A robust and coherent global pattern is discernible of the impacts of climate change on crop productivity that could have consequences for food availability. The stability of whole food systems may be at risk under climate change because of short-term variability in supply. However, the potential impact is less clear at regional scales, but it is likely that climate variability and change will exacerbate food insecurity in areas currently vulnerable to hunger and undernutrition. Likewise, it can be anticipated that food access and utilization will be affected indirectly via collateral effects on household and individual incomes, and food utilization could be impaired by loss of access to drinking water and damage to health. The evidence supports the need for considerable investment in adaptation and mitigation actions toward a "climate-smart food system" that is more resilient to climate change influences on food security.

ackling hunger is one of the greatest challenges of our time (1). Hunger has multiple dimensions and causes, ranging from deficiencies in macro- and micro-nutrients, through short-term shocks on food access, to chronic shortages. Causes range from constraints on the supply of food of sufficient quantity and quality and lack of purchasing power to complex interactions of nutrition with sanitation and infectious diseases leading to poor health. Several of these causes have been addressed in recent decades, and substantial progress has been made in reducing the proportion of the world's undernourished population from an estimated 980 million in 1990-92 to about 850 million in 2010-12 (2). However, from other relevant indicators of nutrition, such as child underweight and stunting and health surveys, an estimated 2 billion people still suffer from micro-nutrient deficiencies today.

The long-term reduction in the prevalence of undernutrition worldwide has slowed since 2007, as a result of pressures on food prices, economic

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