Species Responses to Climate Change

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Introduction

Species are being affected by shifts both in the mean and variability of climate elements, including temperature, precipitation, and their interaction. Species that are effectively able to respond to climate change do so by distributional or phenological shifts, acclimating, or adapting. Evidence of these responses to recent climate change is rapidly accumulating across taxa and regions, compelling research aimed at predicting future ecological and evolutionary responses. Prediction techniques center on using statistical or mechanistic approaches to estimate species niches and to examine shifts in these niches through climate change. These approaches are increasingly incorporating and extending existing physiological, population, and community ecological and evolutionary theory. Another forecasting approach entails identifying the traits of organisms that confer vulnerability to climate change and examining geographic and evolutionary patterns of these traits. The traits can be incorporated in vulnerability frameworks to inform conservation planning.

General Overviews

Most overviews of climate change focus either on the physical science or conservation concerns, but two early-21st-century texts provide overviews of the emerging field of climate change biology. Newman, et al. 2011 focuses on the processes by which species respond to climate change, whereas Hannah 2010 offers a more applied perspective. The texts highlight how many traditional fields of biology need to be integrated to accurately forecast species' responses. These fields include physiology, molecular biology, evolution, population and community ecology, ecosystem ecology, and biogeography. Post 2013 synthesizes the ecological consequences of climate change.

Hannah, L. 2010. *Climate change biology*. Amsterdam: Elsevier.

The text provides an accessible overview of methods for designing reserve networks aimed at minimizing the impacts of climate change on biodiversity.

Newman, J. A., M. Anand, H. A. L. Henry, S. Hunt, and Z. Gedalof. 2011. *Climate change biology*. Cambridge, MA: CABI.

The text provides a more nuanced overview of the processes by which one can scale up from individual physiology to predict climate change impacts.

Post, E. 2013. *Ecology of climate change: The importance of biotic interactions*. Monographs in Population Biology 52. Princeton, NJ: Princeton Univ. Press.

Reviews past, present, and future ecological consequences of climate change, highlighting the role of biotic interactions.

Historical Background

Research into species' responses to climate change has progressed from documenting ecological changes over time to using statistical analyses and models to attribute the response to physical drivers. Efforts to quantify past responses to climate change are being increasingly accompanied by efforts to predict future responses (Pettorelli 2012). Research is shifting from relying on correlation for predicting responses to building models that address the underlying mechanisms. Forecasting techniques are moving beyond predictions focused on the static environmental niches of single species to include species interactions (Kareiva, et al. 1993), dispersal limitations, and evolution. Studies are extending beyond focusing on responses to mean temperatures to additionally considering changes in variability and the incidence of extreme events. Research is also shifting to examine the interaction of multiple physical drivers. This progression has been enabled by the increased availability of climate data; the development of databases compiling species localities, traits, and phylogenies; and improved computational tools.

Kareiva, P. M., J. G. Kingsolver, and R. B. Huey, eds. 1993. *Biotic interactions and global change*. Papers presented at a workshop at the Friday Harbor Laboratories, San Juan Island, WA, in 1991. Sunderland, MA: Sinauer.

This edited volume provides an initial, but still-relevant, examination of how global change will alter species interactions.

Pettorelli, N. 2012. Climate change as a main driver of ecological research. *Journal of Applied Ecology* 49.3: 542–545.

Offers a perspective on past progress and future challenges in understanding ecological responses to climate change, with an eye toward mitigating climate impacts.

Exposure

The magnitude of climate change will vary considerably across locations and seasons. While the magnitude of temperature change is likely to be greatest in the temperate areas, approaches summarized in Tewksbury, et al. 2008 suggest that organisms adapted to more-constant tropical climates may be more sensitive. Reviews in Easterling, et al. 2000 and Smith 2011 illustrate that increases in the incidence of extreme events can have a greater impact on species than shifts in mean conditions. A central challenge for predicting biological impacts was revealed in analyses in Williams, et al. 2007, finding that much of the Earth will experience novel climates by 2100. Early-21st-century analyses have focused on translating climate metrics intro metrics relevant to organisms. Analyses of how fast organisms would need to move geographically and seasonally to keep pace with climate change, such as in Loarie, et al. 2009 and Burrows, et al. 2011, highlight that expected responses are more variable than poleward range shifts and earlier seasonal timing. Chen, et al. 2011 finds that more-pronounced biological responses do tend to correspond to exposure to greater magnitudes of climate warming.

Burrows, M. T., D. S. Schoeman, L. B. Buckley, et al. 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334.6056: 652–655.

Examines the rates at which species would have needed to shift through space and time to keep pace with climate change over the past fifty years. The study finds that rates are spatially variable and are comparable on land and in the ocean despite lesser ocean warming.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high

levels of climate warming. *Science* 333.6045: 1024–1026.

Investigates the rate at which species have shifted in latitude or elevation in response to recent climate change. Rates of shifts vary considerably, but greater responses correspond to greater magnitudes of climate change.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: Observations, modeling, and impacts. *Science* 289.5487: 2068–2074.

Reviews how future changes in extreme events, including increases in the incidence of extreme warm temperatures and intense precipitation events, will interact with shifts in mean climatic conditions to affect species.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* 462.7276: 1052–1055.

Presents an index of how fast organisms would need to move to keep pace with 21st-century climate change, calculated as temperature shifts over time divided by temperature shifts over space. Examines the global distribution of these velocities and the consequences for the residence time of climate in reserves.

Smith, M. D. 2011. An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology* 99.3: 656–663.

Defines extreme climatic events as entailing both an extreme climatic driver and ecological response. Identifies research priorities for understanding the ecological impacts of climate extremes.

Tewksbury, J. J., R. B. Huey, and C. A. Deutsch. 2008. Putting the heat on tropical animals. *Science* 320.5881: 1296–1297.

Summarizes how more-constant tropical climates may lead to thermal specialization and make tropical animals particularly vulnerable to climate warming.

Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America* 104.14: 5738–5742.

Examines the occurrence and global distribution of novel and disappearing climates by 2100 and their potential consequences for biodiversity.

Observed Responses

The literature is rife with examples, compiled in Parmesan 2006, of species responding to recent climate change by shifting their distributions through space and time, acclimating or adapting, or facing declines. Although most literature focuses on species responding directly to thermal cues, Bradshaw and Holzapfel 2010 summarizes how cues including photoperiod additionally drive responses. Meta-analyses in Parmesan and Yohe 2003 and Root, et al. 2003 demonstrate that the majority of species' responses to climate change are consistent with expectations. A subsequent meta-analysis in Rosenzweig, et al. 2008 attributes the responses to human-induced climate change. Poloczanska, et al. 2013 finds that rates of species' responses in marine systems have been at least comparable to those on land, despite lesser warming in the ocean. A challenge in marine systems, highlighted in Harley, et al. 2006 and Hoegh-Guldberg and Bruno 2010, is understanding how the multiple stressors of temperature and acidification interact.

Bradshaw, W. E., and C. M. Holzapfel. 2010. Light, time, and the physiology of biotic response to rapid climate change in animals. *Annual Review of Physiology* 72:147–166.

Summarizes how animals use photoperiod as a cue to time-seasonal activities. Highlights how adaptation of photoperiod cues may facilitate adjusting to climate change.

Harley, C. D. G., A. R. Hughes, K. M. Hultgren, et al. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9.2: 228–241.

An expansive review of abiotic changes in coastal marine systems and how these climate changes will induce biological responses.

Hoegh-Guldberg, O., and J. F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. *Science* 328.5985: 1523–1528.

Reviews how marine systems are responding to increased temperatures and decreased pH, including declines in ocean productivity, shifts in species distributions and food web dynamics, and increases in the prevalence of disease.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.

A comprehensive review demonstrating the concordance between anticipated and observed ecological and evolutionary responses to recent climate change.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421.6918: 37–42.

Global meta-analyses for 1,700 species show that species have been shifting their distributions by 6.1 kilometers (km) per decade and their phenologies by 2.3 days per decade, in directions consistent with expected responses to climate change.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3.10: 919–925.

Finds that 81–83 percent of all observed shifts in distribution, phenology, community composition, abundance, demography, and calcification in marine systems globally are consistent with expected responses to climate change. The rates of distribution and phenological shifts are at least comparable to terrestrial systems.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421.6918: 57–60.

A meta-analysis of time series for diverse taxa, finding that 80 percent of species shifting their phenology in response to climate changes are doing so in the direction expected on the basis of physiological constraints.

Rosenzweig, C., D. Karoly, M. Vicarelli, et al. 2008. Attributing physical and biological impacts to anthropogenic climate change. *Nature* 453.7193: 353–357.

Analyzes the extent to which observed changes in physical and biological systems have been consistent with expected responses to climate change across continents. Finds that about 90 percent of changes (greater than 29,500 data series) have been in the direction expected.

SHIFTS IN RESPONSE TO PALEOCLIMATE CHANGE

How species have responded to past climate changes provides important information for forecasting species' future responses, including insight into the relevant evolutionary processes, as illustrated in Blois and Hadly 2009. Some studies, including Graham, et al. 1996; Davis and Shaw 2001; and Williams and Jackson 2007, reveal the high incidence of species responding idiosyncratically to climate change and the prevalence of no-analogue communities, which provides a central challenge for forecasting. Studies testing ecological forecasting techniques by forecasting past changes, such as Veloz, et al. 2012, have provided crucial information about the ability to extrapolate models into novel climates.

Blois, J. L., and E. A. Hadly. 2009. Mammalian response to Cenozoic climate change. *Annual Review of Earth and Planetary Sciences* 37:181–208.

Reviews the responses of mammals to Cenozoic climate changes, highlighting how climate influences evolutionary processes and how these processes can depend on life history.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292.5517: 673–679.

Reviews how tree distributions shifted in response to Quaternary climate changes. Discusses how species responded individually to climate change, and the influences of genetic variability and adaptation.

Graham, R. W., E. L. Lundelius Jr., M. A. Graham, et al. 1996. Spatial response of mammals to Late Quaternary environmental fluctuations. *Science* 272.5268: 1601–1606.

Uses mammal fossil localities to document how distribution shifts differed in timing, direction, and rate in response to Late Quaternary climate fluctuations.

Veloz, S. D., J. W. Williams, J. L. Blois, F. He, B. Otto-Bliesner, and Z. Liu. 2012. No-analog climates and shifting realized niches during the Late Quaternary: Implications for 21st-century predictions by species distribution models. *Global Change Biology* 18.5: 1698–1713.

Uses fossil pollen data to show that species distribution models perform poorly when species shift their realized niches, as has occurred since the late glacial period.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5.9: 475–482.

An assessable and informative review of how communities without compositional analogues have formed, frequently in response to past climate changes. Suggests that novel environments are likely to drive no-analogue communities in the future and will challenge many ecological models.

SHIFTS THROUGH TIME

Changes in seasonal timing are among the most prominent observed responses to climate change, as reviewed in Cleland, et al. 2007 and Pau, et al. 2011. Extensive phenological data sets, including those presented in Fitter and Fitter 2002; Menzel, et al. 2006; Lenoir, et al. 2008; and Thackeray, et al. 2010, are starting to reveal how the characteristics of organisms influence the magnitude of phenological shifts. One challenge for understanding the impact of phenological shifts on the viability of species is that such shifts may indicate either effective acclimation or species vulnerability. Consistent with the former, Cleland, et al. 2012 shows that phenological tracking can maintain fitness. Much of our understanding of the mechanisms underlying phenological shifts are from warming experiments. However, Wolkovich, et al. 2012 suggests that experiments may underestimate phenological shifts.

Cleland, E. E., J. M. Allen, T. M. Crimmins, et al. 2012. Phenological tracking enables positive species responses to climate change. *Ecology* 93.8: 1765–1771.

Synthesizes results from experiments on terrestrial warming to show that those plant species that phenologically track climate change tend to experience performance (biomass, percent cover, number of flowers, or individual growth) increases, whereas those that do not track tend to experience performance declines.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* 22.7: 357–365.

Reviews approaches for examining plant phenological responses to climate change, at multiple scales. Addresses how these approaches can be used to understand the mechanisms driving phenological shifts and to predict the consequences of future shifts for ecosystem productivity.

Fitter, A. H., and R. S. R. Fitter. 2002. Rapid changes in flowering time in British plants. *Science* 296.5573: 1689–1691.

Finds that the average first-flowering date of 385 British plant species has advanced by 4.5 days between 1991 and 2000. These phenological shifts varied between species according to their life history.

Lenoir, J., J.-C. Gégout, P. A. Marquet, P. de Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320.5884: 1768–1771.

Uses large-scale floristic inventories in western Europe to show that the optimal elevation of 171 forest plant species had shifted upward at a rate of 29 meters per decade over the 20th century. Montane and grassy species, with fast life cycles, exhibited the most-pronounced shifts.

Menzel, A., T. H. Sparks, N. Estrella, et al. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12.10: 1969–1976.

Uses an extensive and systematic phenological monitoring network to demonstrate that 78 percent of plant-leafing, flowering, and fruiting records advanced across Europe over the recent period of climate change. The average spring/summer advance was 2.5 days per decade and 2.5 days per °C.

Pau, S., E. M. Wolkovich, B. I. Cook, et al. 2011. Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology* 17.12: 3633–3643.

Outlines a framework for using species traits and phylogeny to predict phenological responses to climate variability. The authors predict that high-latitude and early-season species will be most sensitive to climate.

Thackeray, S. J., T. H. Sparks, M. Frederiksen, et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* 16.12: 3304–3313.

Documents phenological shifts for 726 UK taxa and demonstrates slower rates for higher trophic levels, raising concern over the potential for increasing phenological asynchrony.

Wolkovich, E. M., B. I. Cook, J. M. Allen, et al. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485.7399: 494–497.

Shows that warming experiments, which are often used to predict phenological shifts, may substantially underpredict shifts in flowering and leafing time as compared to long-term observations.

SHIFTS THROUGH SPACE

Distribution shifts are another well-established response to climate change, as evidenced in Sorte, et al. 2010. Studies of range shifts both in marine and terrestrial systems, including Perry, et al. 2005 and La Sorte and Thompson 2007, are beginning to address the characteristics of organisms that determine the occurrence and extent of range shifts. One compelling way to document distribution shifts, as illustrated in Barry, et al. 1995; Moritz, et al. 2008; and Tingley, et al. 2009, is to repeat historical surveys.

Barry, J. P., C. H. Baxter, R. D. Sagarin, and S. E. Gilman. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267.5198: 672–675.

Concurrent with increases in shore temperature between 1931 and 1994, the distribution of rocky intertidal species in California shifted northward. The abundance of southern species increased whereas the abundance of northern species decreased.

La Sorte, F. A., and F. R. Thompson. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88.7: 1803–1812.

Bird species in North America shifted their wintering northern boundary (1.48 km/yr), center of occurrence (0.45 km/yr), and center of abundance (1.03 km/yr) poleward between 1975 and 2004. Shifts were attributed both to climate change and other anthropogenic activities.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322.5899: 261–264.

Half of montane small-mammal species shifted their distribution upward during a roughly 3°C increase in minimum temperatures since the early 20th century. Species' responses were idiosyncratic, but low- and high-elevation species tended to experience distribution expansions and contractions, respectively.

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* 308.5730: 1912–1915.

The distributions of two-thirds of North Sea fish species have shifted in mean latitude or depth over twenty-five years of increases in sea temperature. Species with faster life cycles and smaller body sizes exhibited more-pronounced shifts.

Sorte, C. J. B., S. L. Williams, and J. T. Carlton. 2010. Marine range shifts and species introductions: Comparative spread rates and community impacts. *Global Ecology and Biogeography* 19.3: 303–316.

Three-quarters of the range shifts among marine species were found to be poleward, consistent with expected responses to climate change. Range shifts were observed to occur more rapidly in oceans than on land. Climate-associated range shifts are compared to species introductions.

Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America* 106.S2: 19637–19643.

Among bird species along montane elevation transects, 90.6 percent tracked their climatic niche through climate change over the 20th century.

SHIFTS IN ABUNDANCE AND CONDITION

Shifts in abundance and other indicators of the condition and fitness of organisms are revealing the mechanisms by which species respond to climate change. For example, Altermatt 2009 documents increases in the number of generations that species are able to complete annually, confirming physiologically based expectations for responses to climate change. Ozgul, et al. 2009 and Ozgul, et al. 2010 investigate how shifts in growth rates and the length of the growing season influence body size and population dynamics. Huey, et al. 2009 and Jiguet, et al. 2010 investigate the consequences of organismal physiology for the incidence of thermal stress and abundance, respectively. Although abundance trends can be difficult to interpret, Møller, et al. 2008 demonstrates that they can provide important information about the fitness consequences of climate change. An additional important issue, reviewed in Altizer, et al. 2013, is how climate change will alter disease risk.

Altermatt, F. 2009. Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences* 277.1685: 1281–1287.

Among species of butterflies and moths in central Europe, 72 percent have increased the number of generations completed annually, concurrent with climate warming, since 1980.

Altizer, S., R. S. Ostfeld, P. T. J. Johnson, S. Kutz, and C. D. Harvell. 2013. Climate change and infectious diseases: From evidence to a predictive framework. *Science* 341.6145: 514–519.

Proposes an ecophysiological framework to evaluate how climate drivers influence disease prevalence and impact.

Huey, R. B., C. A. Deutsch, J. J. Tewksbury, et al. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B: Biological Sciences* 276.1664: 1939–1948.

Analyzes the thermal biology of lizards across latitude and suggests thermally specialized tropical lizards may be more vulnerable to warming. The authors support this by estimating shifts in body temperatures of lowland tropical lizards as well as associated decreases in performance over recent decades of climate warming.

Jiguet, F., R. D. Gregory, V. DeVictor, et al. 2010. Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology* 16.2: 497–505.

Among 110 breeding bird species, those with the lowest thermal maxima showed the most-pronounced abundance declines in Europe between 1980 and 2005.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America* 105.42: 16195–16200.

Analyses of long-term trends for one hundred breeding bird species demonstrate that species that did not advance their spring migration declined in abundance between 1990 and 2000, whereas those species that did so tended to exhibit stable or increasing populations.

Ozgul, A., D. Z. Childs, M. K. Oli, et al. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466.7305: 482–485.

Alpine marmots have emerged from hibernation and weaned their young progressively earlier since 1976. This has lengthened their growing season and has increased their mass, leading to decreased mortality and increased population sizes.

Ozgul, A., S. Tuljapurkar, T. G. Benton, J. M. Pemberton, T. H. Clutton-Brock, and T. Coulson. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science* 325.5939: 464–467.

Demonstrates that declines in Soay sheep body size that were associated with environmental change results from decreased growth rates rather than phenotypic selection.

ADAPTATION AND ACCLIMATION

A review in Gienapp, et al. 2008 highlights that studies are increasingly providing evidence of organisms responding to climate change via acclimation and adaptation. One example of historical data evidencing phenotypic shifts over time is provided in Karell, et al. 2011. Replicating experiments across decades can reveal genetic changes (van Asch, et al. 2013), and quantitative genetic experiments can demonstrate selection underlying phenotypic shifts (Anderson, et al. 2012). Rubidge, et al. 2012 provides an example of how genetic changes can be detected by comparing historical and modern specimens. Hofmann and Todgham 2010 reviews the numerous physiological mechanisms by which organisms may respond to climate change. Documenting such processes is challenging. However, using empirical data to define the parameters of evolutionary models, as exemplified by Gienapp, et al. 2013, can estimate the extent to which plasticity and adaptation will enable tracking climate change. Lau and Lennon 2012 provides an example of how the evolution of interacting species with rapid life cycles may influence responses to environmental change.

Anderson, J. T., D. W. Inouye, A. M. McKinney, R. I. Colautti, and T. Mitchell-Olds. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B:*

Biological Sciences 279.1743: 3843–3852.

The authors integrate a thirty-eight-year field survey of a montane plant with a quantitative genetic experiment to attribute a portion of the advancement in flowering associated with warmer temperatures and earlier snowmelt to directional selection.

Gienapp, P., M. Lof, T. E. Reed, J. McNamara, S. Verhulst, and M. E. Visser. 2013. Predicting demographically sustainable rates of adaptation: Can great tit breeding time keep pace with climate change? _Philosophical Transactions of the Royal Society B: Biological Sciences_ 368.1610: 20120289.

The authors used long-term phenological data for great tits to define the parameters of evolutionary models. The predicted critical rate of climate change that breeding time can track via adaptation and plasticity is low relative to projections.

Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä. 2008. Climate change and evolution: Disentangling environmental and genetic responses. _Molecular Ecology_ 17.1: 167–178.

An overview of the mechanism and evidence of genetic and plastic responses to climate change.

Hofmann, G. E., and A. E. Todgham. 2010. Living in the now: Physiological mechanisms to tolerate a rapidly changing environment. _Annual Review of Physiology_ 72:127–145.

An overview of the physiological mechanisms by which organisms can acclimate to environmental change. Highlights the potential synergistic interactions among multiple environmental stressors.

Karell, P., K. Ahola, T. Karstinen, J. Valkama, and J. E. Brommer. 2011. Climate change drives microevolution in a wild bird. _Nature Communications_ 2.2: 208.

The authors demonstrate that dark plumage coloration in tawny owls is heritable and selected against in snowy winters. Milder winters in recent decades have reduced selection against the brown morph and have increased their frequency in populations.

Lau, J. A., and J. T. Lennon. 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. _Proceedings of the National Academy of Sciences of the United States of America_ 109.35: 14058–14062.

A multigenerational experiment examining responses of plants and soil microbial communities to drought stress. Plant evolutionary responses were limited, but plant fitness was governed by rapid responses of the soil microbial communities.

Rubidge, E. M., J. L. Patton, M. Lim, A. C. Burton, J. S. Brashares, and C. Moritz. 2012. Climate-induced range contraction drives genetic erosion in an alpine mammal. _Nature Climate Change_ 2.4: 285–288.

A range contraction over a century of warming decreased genetic diversity and increased genetic subdivision in an alpine chipmunk. A related chipmunk maintained a stable distribution and did not experience genetic changes.

van Asch, M., L. Salis, L. J. M. Holleman, B. van Lith, and M. E. Visser. 2013. Evolutionary response of the egg hatching date of a herbivorous insect under climate change. _Nature Climate Change_ 3.3: 244–248.

The authors integrate long-term phenological observations and experiments replicated over time to demonstrate selection for delayed egg-hatching date in response to climate change. Selection has reduced asynchrony between winter moths and their food plant.

Predicting Future Responses

Theoretical Models of genetic and phenotypic adaptation elegantly illustrate the determinants of species' responses but are difficult to parameterize and apply to empirical systems. Consequently, the most common ecological-forecasting approach entails using locality and environmental data to estimate statistical correlations describing a species' environmental niche. The mixed success of Environmental-Niche Models when forecasting responses to past climate changes is inspiring models that include additional biological details describing species' responses to the environment and each other. Mechanistic-Niche Models use organismal traits to estimate a species' fundamental niche. Related modeling approaches generalize the physiology of organisms or use demographic data to estimate vital rates.

THEORETICAL MODELS

Climate change provides a dynamic test of much existing population and community ecology theory. Sexton, et al. 2009 reviews the determinants of range limits crucial to species' responses to environmental change. Models of how gene flow (Kirkpatrick and Barton 1997) and species interactions (Case and Taper 2000) set range limits are particularly pertinent. Whether species will adapt to track climate change is a central question posed in Visser 2008 and Hoffmann and Sgrò 2011. A model in Lynch and Lande 1993 investigates limits to rates of adaptation, and Chevin, et al. 2010 extends the model to incorporate how plasticity modifies these rates. An ongoing challenge is in devising techniques to define parameters of and to apply theoretical models.

Case, T. J., and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *American Naturalist* 155.5: 583–605.

Expands the model in Kirkpatrick and Barton 1997 to include species interactions. Demonstrates that interactions with a better-adapted competitor can displace marginal populations, increasing asymmetry in gene flow and fixing range limits.

Chevin, L.-M., R. Lande, and G. M. Mace. 2010. Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology* 8.4: e1000357.

Expands the model in Lynch and Lande 1993 to account for phenotypic plasticity. Examines how plasticity and its cost influence the critical rate of environmental change.

Hoffmann, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. *Nature* 470.7335: 479–485.

Addresses how to identify when evolution will occur in response to climate change and how we can build realistic and empirically informed evolutionary models to identify for which species limited evolutionary capacity will confer vulnerability to climate change.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. *American Naturalist* 150.1: 1–23.

Theory examining how gene flow, adaptation, and selection interact to set range limits along an environmental gradient. Highlights that gene flow from large, well-adapted interior populations may hinder adaption in marginal populations.

Lynch, M., and R. Lande. 1993. Evolution and extinction in response to environmental change. Paper presented at a workshop at the Friday Harbor Laboratories, San Juan Island, WA, in 1991. In *Biotic interactions and global change*. Edited by P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, 234–250. Sunderland, MA: Sinauer.

A foundational evolutionary model describing the lag of phenotypes behind an optima in changing environments. The model estimates the critical rate of environmental change a population can cope with through adaptation.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.

A comprehensive overview of the ecological and evolutionary theories underlying our understanding of range limits. Documents the limited number of experiments that have tested these theories.

Visser, M. E. 2008. Keeping up with a warming world: Assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences* 275.1635: 649–659.

Addresses whether adaptation will be sufficiently rapid to track climate change. Reviews the mechanisms determining rates of adaptation and how empirical studies can inform predictions of evolutionary rates.

ENVIRONMENTAL-NICHE MODELS

Environmental-niche models (ENMs, or correlative species distribution models, SDMs), which estimate a species' environmental niche on the basis of localities and assume that the species will remain in the niche as it shifts through climate change, are a predominant method of prediction and are reviewed in Franklin 2009. Numerous reviews, including Pearson and Dawson 2003 and Elith and Leathwick 2009, describe the methodology and challenges faced for implementing ENMs. Model performance has been assessed by assembling large data sets of current distributions (Elith, et al. 2006), by simulating species (Elith and Graham 2009), and by hindcasting past range shifts (Araujo, et al. 2005). Thomas, et al. 2004 is a prominent example of applying ENMs to predict the global biodiversity implications of climate change

Araujo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. Validation of species–climate impact models under climate change. *Global Change Biology* 11.9: 1504–1513.

An influential initial attempt to validate ENMs by hindcasting the responses of UK birds to recent climate change. The models exhibited mixed performance in independent validation, but measures of performance on nonindependent data were higher.

Elith, J., and C. H. Graham. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography* 32.1: 66–77.

Uses simulated species to compare the performance of ENMs and to identify the source of performance differences.

Elith, J., C. H. Graham, R. P. Anderson, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29.2: 129–151.

A comprehensive comparison of the implementation and performance of ENMs for numerous species across multiple regions.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697.

A thorough review of past implementations of and future challenges for ENMs.

Franklin, J. 2009. *Mapping species distributions: Spatial inference and prediction*. Ecology, Biodiversity and Conservation. Cambridge, UK: Cambridge Univ. Press.

A thorough introduction to ENMs.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography* 12.5: 361–371.

Evaluates critiques of ENMs and discusses strategies for their effective implementation.

Thomas, C. D., A. Cameron, R. E. Green, et al. 2004. Extinction risk from climate change. *Nature* 427:145–148.

An influential and controversial implementation of ENMs to predict the global extinction risk posed by climate change.

DEMOGRAPHIC MODELS

Using long-term time series to track demography has provided important insight into how climate change alters fitness. Such models have highlighted the importance of considering individual variation (Clark, et al. 2012) and the potential for demographic compensation (Doak and Morris 2010). Demography provides a powerful basis for predicting future responses to climate change (Jenouvrier, et al. 2009) and can be integrated with other modeling techniques to improve their mechanistic basis (Keith, et al. 2008).

Clark, J. S., D. M. Bell, M. Kwit, A. Stine, B. Vierra, and K. Zhu. 2012. Individual-scale inference to anticipate climate-change vulnerability of biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367.1586: 236–246.

Discusses the importance of individual-scale variability for species interactions and outlines how modeling the demographic processes of individuals can provide insight into the biodiversity implications of global change.

Doak, D. F., and W. F. Morris. 2010. Demographic compensation and tipping points in climate-induced range shifts. *Nature* 467.7318: 959–962.

The authors incorporated long-term data for tundra plants in demographic models to investigate responses to climate change across their distributions. They find that lower survival and recruitment within southern populations are being countered by higher individual growth rates (potentially associated with expanded growing seasons), which have stabilized the distribution.

Jenouvrier, S., H. Caswell, C. Barbraud, M. Holland, J. Strœve, and H. Weimerskirch. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences of the United States of America* 106.6: 1844–1847.

Uses a long-term demographic data set for Antarctic penguins to predict how climate change will influence the future population viability. The model suggests that an increased frequency of warm events associated with diminished sea ice will reduce population viability.

Keith, D. A., H. R. Akçakaya, W. Thuiller, et al. 2008. Predicting extinction risks under climate change: Coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* 4.5: 560–563.

Introduces a method for considering both climate-induced changes in habitat suitability and population dynamics, by integrating stochastic population models and ENMs.

PHYSIOLOGICAL MODELS

Helmuth, et al. 2002 provides a compelling example of how organismal phenotypes interact with local microclimates to produce complex patterns of thermal stress. Thermal conditions drive both local and broad-scale patterns of thermal adaptation (Chown and Gaston 2008, Angilletta 2009) that can be used to predict responses to climate change (Kingsolver 2009). Mechanisms underlying these predictions include the temperature dependence of metabolism (Dillon, et al. 2010), thermal limits on activity time (Sinervo, et al. 2010), the temperature dependence of fitness (Deutsch, et al. 2008), and the extent to which organisms fill their potential thermal niche (Sunday, et al. 2012).

Angilletta, M. J., Jr. 2009. *Thermal adaptation: A theoretical and empirical synthesis*. Oxford Biology. Oxford: Oxford Univ. Press.

A comprehensive treatment of thermal adaptation and its implications for species' responses to climate change. The book focuses on interfacing theoretical mechanisms and empirical patterns.

Chown, S. L., and K. J. Gaston. 2008. Macrophysiology for a changing world. *Proceedings of the Royal Society B: Biological Sciences* 275.1642: 1469–1478.

Reviews how macrophysiology—the investigation of variation in physiological traits over large geographical, temporal, and phylogenetic scales—can provide insight into how species will respond to environmental change.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 105.18: 6668–6672.

Uses seasonality to generalize empirical fitness curves for insects across latitudes and to predict the fitness implications of climate change. Finds that thermal specialization may lead to more-pronounced fitness declines in the tropics, despite a lesser magnitude of warming.

Dillon, M. E., G. Wang, and R. B. Huey. 2010. Global metabolic impacts of recent climate warming. *Nature* 467.7316: 704–706.

Quantifies the impacts of climate change on metabolic rates globally. Finds that temperature's nonlinear effects on metabolic rates result in large metabolic impacts in the tropics, despite the small magnitude of temperature change.

Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate change and

latitudinal patterns of intertidal thermal stress. *Science* 298.5595: 1015–1017.

Examines how microclimate variation can cause the body temperatures of organisms to depart from air temperatures, causing thermal stress to occur as a mosaic rather than a latitudinal cline.

Kingsolver, J. G. 2009. The well-temperatured biologist. *American Naturalist* 174.6: 755–768.

Explores thermal adaptation across levels of biological organization, and its relevance for predicting species' responses to climate change.

Sinervo, B., F. Méndez-de-la-Cruz, D. B. Miles, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328.5980: 894–899.

Develops relationships between the activity time available to lizards and extinction risk. Validates the relationships for the local extinction of Mexican lizards since 1975 and projects them to predict future lizard extinction resulting from climate change.

Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2012. Thermal tolerance and the global redistribution of animals. *Nature Climate Change* 2.9: 686–690.

Examines the degree to which terrestrial ectotherms fill their potential latitudinal ranges, estimated from their limits of thermal tolerance. The authors find that marine ectotherms more fully occupy their potential latitudinal boundaries compared to terrestrial ectotherms. Recent climate-induced range shifts correspond to the predictions.

MECHANISTIC-NICHE MODELS

Helmuth, et al. 2005 makes a strong case that considering the details of the interaction between organisms and their environment can be crucial to accurately predicting species' responses to climate change. Mechanistic-niche models (MNMs), reviewed in Kearney and Porter 2009; Buckley, et al. 2010; and Dormann, et al. 2012, aim to describe the properties of organisms and the processes by which they interact with the environment, to predict species distributions and their responses to climate change. One factor propelling MNMs is their potential to be extrapolated into novel environments.

Buckley, L. B., M. C. Urban, M. J. Angilletta, L. G. Crozier, L. J. Rissler, and M. W. Sears. 2010. Can mechanism inform species' distribution models? *Ecology Letters* 13.8: 1041–1054.

The authors compare the performance of ENMs and MNMs for two focal species. They find that the approaches perform similarly when predicting current distributions, but the MNMs predict more-pronounced and individualistic responses to climate change.

Dormann, C. F., S. J. Schymanski, J. Cabral, et al. 2012. Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography* 39.12: 2119–2131.

A point-by-point comparison of ENMs and MNMs for two focal species.

Helmuth, B., J. G. Kingsolver, and E. Carrington. 2005. Biophysics, physiological ecology, and climate change: Does mechanism matter? *Annual Review of Physiology* 67:177–201.

A comprehensive review of how considering the mechanistic details of physiological performance can be crucial for understanding the ecological impacts of climate change.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12.4: 334–350.

The authors conceptually compare ENMs and MNMs and discuss situations when MNMs may be particularly valuable.

Influence of Biotic Interactions

Most current approaches for predicting species' responses to climate change are focused on the environmental niches of individual species, but emerging evidence compiled in DeLucia, et al. 2012 and Hegland, et al. 2009 points to the importance of factors such as biotic interactions and dispersal limitations. For example, Urban, et al. 2012 illustrates how competition between species and dispersal differences can create no-analogue communities. A synthetic review in Tylianakis, et al. 2008 highlights how the complexity of multiple environmental stressors interacting with communities poses a challenge for predicting species' responses. Gilman, et al. 2010 proposes that identifying the key interactions provides one tractable way to predict how biotic interactions influence responses to climate change. Considering the relative timing of species across their phenology can provide insight into how climate change will shift species interactions (Yang and Rudolf 2010), as can evaluating phenological shifts relative to those of interacting species (Visser and Both 2005).

DeLucia, E. H., P. D. Nabity, J. A. Zavala, and M. R. Berenbaum. 2012. Climate change: Resetting plant-insect interactions. *Plant Physiology* 160.4: 1677–1685.

A review of how climate change may disrupt interactions between plants and insects.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology & Evolution* 25.6: 325–331.

Proposes a framework for predicting alterations in community interactions due to climate change, by identifying the most-important interactions and analyzing them as community modules.

Hegland, S. J., A. Nielsen, A. Lázaro, A.-L. Bjerknes, and Ø. Totland. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12.2: 184–195.

Reviews how climate change can alter plant-pollinator interactions. Focuses on the incidence and consequences of distributional and phenological mismatches.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11.12: 1351–1363.

The authors compile data from 688 studies to examine how global change alters species interactions. They find that the alterations vary in magnitude and direction and that the interaction of multiple stressors creates challenges in predicting responses.

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: Competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B: Biological Sciences* 279.1735: 2072–2080.

Develops simple models to provide examples of how competition and dispersal differences among species along elevation gradients can create no-analogue communities.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences* 272.1581: 2561–2569.

Examines the occurrence of phenological asynchrony as a result of climate change and advocates examining phenology relative to that of other species.

Yang, L. H., and V. H. W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters* 13.1: 1–10.

Proposes a framework for examining phenology across ontogeny, to understand how phenological shifts will alter species interactions.

INSIGHT FROM EXPERIMENTS

Warming experiments can address how direct and indirect effects within communities interact to determine species' responses, as exemplified by Harmon, et al. 2009. An experiment in Suttle, et al. 2007 demonstrates that indirect effects of climate change can sometimes reverse direct effects. Experiments exploring the physiology of species interactions, such as those in Harley 2011, address the mechanisms by which species interactions can modify responses to climate change. Transplant experiments, such as in Pelini, et al. 2009, can address how species interactions can alter range shifts.

Harley, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science* 334.6059: 1124–1127.

Integrates experiments and surveys to demonstrate how warming reduces mussels' spatial refuge from starfish on rocky shores. Examines the mechanisms by which global change may alter species richness.

Harmon, J. P., N. A. Moran, and A. R. Ives. 2009. Species response to environmental change: Impacts of food web interactions and evolution. *Science* 323.5919: 1347–1350.

Experimentally examines how direct and indirect effects interact to determine how food webs respond to environmental change.

Pelini, S. L., J. D. K. Dzurisin, K. M. Prior, et al. 2009. Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. *Proceedings of the National Academy of Sciences of the United States of America* 106.27: 11160–11165.

Uses transplant experiments to demonstrate how host plant availability influences butterfly range shifts in response to environmental change.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing

climate. *Science* 315.5812: 640–642.

A grassland-warming experiment reveals how species interactions can alter responses to climate change and how the balance of direct and indirect effects can vary over time.

Vulnerability and Conservation

Ecologists have long outlined characteristics expected to confer sensitivity to climate change, but these vulnerability frameworks have seldom been tested. Key aspects of sensitivity, incorporated in a framework in Williams, et al. 2008, include biotic vulnerability, exposure to climate change, potential evolutionary and acclimatory responses, and the potential efficacy of management strategies. Huey, et al. 2012 reviews how organismal characteristics can serve as proxies for difficult-to-quantify aspects of vulnerability related to behavior, physiology, and adaptation. Early-21st-century attempts to examine how distribution and phenological shifts are conserved across phylogeny and functionally similar species, compiled in Buckley and Kingsolver 2012, have achieved mixed success. An analysis in Angert, et al. 2011 reveals that species traits tend to predict a modest, but significant, percent of the variation in the magnitude of species' responses. Davis, et al. 2010 demonstrates that phylogeny can provide an effective proxy for traits, such that closely related species may respond similarly to climate change because of having phylogenetically conserved traits. Improving understanding of species vulnerability to climate change is facilitating conservation planning to maintain biodiversity (Dawson, et al. 2011) in the face of uncertainty (Lawler, et al. 2010).

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? *Ecology Letters* 14.7: 677–689.

Finds that species traits can account for a significant, but modest, amount of variation in the magnitude of species range shifts.

Buckley, L. B., and J. G. Kingsolver. 2012. Functional and phylogenetic approaches to forecasting species' responses to climate change. *Annual Review of Ecology, Evolution, and Systematics* 43:205–226.

Examines how organismal characteristics such as thermal and hydric limits, seasonal timing and duration of the life cycle, ecological breadth and dispersal capacity, and fitness and evolutionary potential can be used to predict species' responses to climate change.

Davis, C. C., C. G. Willis, R. B. Primack, and A. J. Miller-Rushing. 2010. The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1555: 3201–3213.

Reviews how phenological shifts tend to be phylogenetically conserved.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: Biodiversity conservation in a changing climate. *Science* 332.6025: 53–58.

Reviews how vulnerability frameworks can be used in conservation planning aimed at maintaining biodiversity through global change.

Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012. Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal*

***Society B: Biological Sciences* 367.1596: 1665–1679.**

Evaluates the potential to incorporate proxies for behavior, physiology, and adaptation in vulnerability frameworks of climate change.

Lawler, J. J., T. H. Tear, C. Pyke, et al. 2010. Resource management in a changing and uncertain climate. *Frontiers in Ecology and the Environment* 8.1: 35–43.

Reviews conservation-planning approaches for dealing with the uncertain outcomes of climate change.

Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann, and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* 6.12: e325.

Proposes a framework for assessing the vulnerability of species to climate change.

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