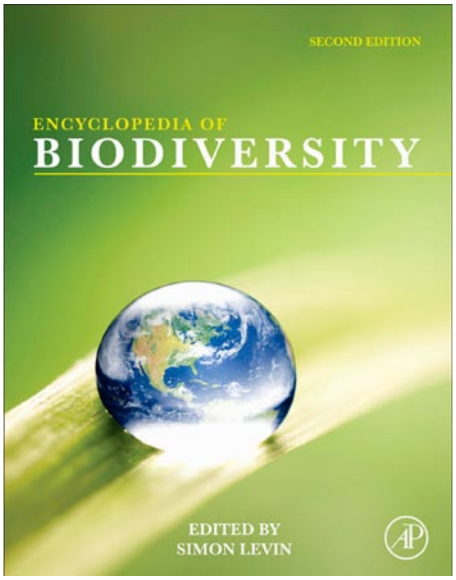




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# Climate Change: Anticipating and Adapting to the Impacts on Terrestrial Species

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## Glossary

**Adaptation** Actions that ameliorate the impacts of climate change on systems or species or that allow for systems and species to take advantage of climatic changes.
**Adaptive management** An iterative process of management and monitoring that treats management actions as experiments, the results of which inform changes in management actions.
**Assisted colonization** The translocation of species outside of their native range to allow them to track changes in climate.
**Co-benefits** Beneficial outcomes for human or natural systems of adaptation or strategies designed to address one or the other system.
**Mitigation** Actions designed to reduce the amount that the climate will change. These actions generally involve reducing greenhouse gas emissions and sequestering carbon dioxide ($CO_2$).
**Phenology** The timing of ecological events.
**Resilience** The ability of a system or species to return to its initial condition after perturbation by climate change.
**Resistance** The ability of a system or species to remain largely unchanged in the face of climate change.
**Triage** A system of prioritization for making decisions when resources are scarce and the need for responses is widespread.

## Introduction

Climate change is poised to significantly alter ecological systems. Recent climatic changes have resulted in clear shifts in species distributions and the timing of ecological events (Parmesan, 2006). Although range shifts and changes in phenology are the two most well documented effects of recent climatic changes, there are a myriad of other ways in which changes in climate have affected and will likely affect terrestrial species. Among other things, climate change has the potential to alter population processes, interspecific interactions, and the impact of diseases and parasites. All of these effects have been documented to some degree.

The magnitude and rate of climatic changes projected for the coming century will provide challenges for many terrestrial species (IPCC, 2007a, b). Addressing these challenges will require some understanding of how species will likely respond to projected changes. There are several tools that can help scientists, managers, and planners anticipate the impacts of climate change on terrestrial species. These tools range from understanding historical patterns and conducting experiments to developing complex simulation models to forecast potential impacts.

An understanding of how species will likely respond to climate change is critical for developing management strategies and policies to maintain populations, protect species, and sustain ecosystem functions in a changing climate. Such approaches are generally referred to as adaptation strategies. The Intergovernmental Panel on Climate Change (2007a) has defined adaptation as "the adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities." Many adaptation strategies have been proposed for terrestrial ecological systems and specifically for terrestrial species. The majority of these strategies are broad recommendations or general concepts, but some are more specific actions.

The following sections provide both an overview of some of the impacts of climate change and how they can be anticipated and a review of the adaptation strategies that have been proposed for addressing these impacts.

## Anticipating Impacts

There are many potential impacts of climate change on terrestrial species. The following sections concentrate on six types of impacts – impacts on phenology, range shifts, population processes, interspecific interactions, diseases and parasites, and interactions with other, nonclimatic stressors. Each section provides an overview of impacts and approaches for anticipating those impacts.

### Phenology

One of the most widely observed ecological effects of climate change is a shift in phenology – the seasonal timing of life history events, such as flowering, egg hatching, migration, and senescence. For centuries, people have been observing phenology for agricultural and religious reasons, as well as simply to record changing seasons. For example, grape harvest dates have been tracked for the past 500 years across Europe (Menzel, 2005) and the appearance of spring cherry blossoms has been recorded since the fifteenth century in Japan (Menzel and Dose, 2005). In general, these and other historical data suggest a shift in the seasonal timing of biological events as temperatures have risen over the past century. Spring and summer events, including frog spawning, bird nesting, and

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leaf unfolding, are occurring earlier, and the vegetative growing season has lengthened (Parmesan, 2006; Feehan *et al.*, 2009; Thackeray *et al.*, 2010). These changes have occurred rapidly and have been particularly strong at high latitudes, where warming has been the greatest (Parmesan, 2006; Feehan *et al.*, 2009). From 1976 to 2005, phenology of plants, invertebrates, and vertebrates in terrestrial, marine, and freshwater environments advanced, on average, by 11.7 days (0.38 days per year) (Thackeray *et al.*, 2010).

Although there has been an overall advancement in the timing of biological events, significant variation exists in patterns of phenological shifts across ecosystems, species, trophic levels, and functional groups. Of terrestrial organisms, plants have shown the most rapid rate of change (0.58 days per year from 1976 to 2005), and vertebrates have shown the slowest (0.25 days per year) (Thackeray *et al.*, 2010). These varying rates of change suggest that asynchronies may develop between interacting species, such as predators and their prey or plants and their pollinators. Indeed, asynchronies, or "phenological mismatches," have already been observed and, in some cases, have resulted in both reductions in individual fitness and declining population sizes (Parmesan, 2006; Forrest and Miller-Rushing, 2010; Miller-Rushing *et al.*, 2010).

By combining historical relationships between phenologies and climate with future climate projections, research efforts have begun to forecast how future changes in climate will affect phenology and the consequences of these potential phonological shifts (Memmott *et al.*, 2010; Ogden *et al.*, 2008a, b; Tobin *et al.*, 2008; Caffarra and Eccel, 2011). These forecasts project continued shifts toward earlier arrival of spring events, particularly at high altitudes (Caffarra and Eccel, 2011). Forecasts suggest that climate-induced phenological shifts can have major impacts on species interactions and communities, even when complete phenological mismatches do not occur (Fabina *et al.*, 2010).

Forecasting future phenological shifts is difficult, because the understanding is based largely on correlative observational studies. In many cases, there is no mechanistic understanding of controls over phenology and the degree to which it is controlled by climate. Genetics and nonclimatic cues such as photoperiod also affect phenology (Forrest and Miller-Rushing, 2010; Valtonen *et al.*, 2011). Furthermore, observational data have been biased toward plants, and the knowledge of trends in other organisms is limited. Even when extensive data and understanding are present, it may be problematic to assume that future trends will follow those in the past. For example, in the Tibetan Plateau, from 1982 to 2006, trends in spring vegetation phenology initially advanced concurrent with warming patterns, but started retreating in the mid-1990s in spite of continued warming (Yu *et al.*, 2010). The authors conclude that warm winter conditions caused a delay in spring phases due to chilling requirements. Species- and site-level variations in the magnitude and direction of phenological responses to changes in temperature highlight the need for further research on climate-induced shifts in phenology. In particular, mechanistic studies that determine the influence of climate on phenology and research on mammals, amphibians, fungi, and other understudied organisms are needed to improve the ability to anticipate future phenological changes.

## Range Shifts

Climatic factors broadly determine species distributions, and therefore, climatic changes can cause associated changes in species distributions, or range shifts. Over the past century, both altitudinal and latitudinal range shifts in temperate- and tropical–terrestrial species have accompanied climatic changes (Parmesan and Yohe, 2003; Parmesan, 2006; Walther *et al.*, 2002; Root *et al.*, 2003). As the climate changes, species expand their ranges to occupy previously climatically unsuitable areas (Parmesan, 2006). Conversely, climatic changes may reduce the climatic suitability of species' current distributions, resulting in range contractions through local population extinctions (Parmesan *et al.*, 1999). The combination of range expansions into regions of newly suitable climate and range contractions away from regions of unsuitable climate can result in overall shifts in species ranges (Pearson and Dawson, 2003; Parmesan *et al.*, 1999).

Range shifts have been documented for plants, insects, birds, mammals, amphibians, and reptiles in tropical, temperate, and arctic regions. Overall, the magnitude and direction of these shifts have been consistent with climatic changes and tend to be poleward and/or upward in elevation, with an average shift of 6.1 km poleward or 6.1 m upward per decade (Parmesan and Yohe, 2003). Despite the general trend of upward and poleward range shifts, distributional responses to climate change are largely individualistic, with some species showing no change in their distributions despite warming and others showing shifts inconsistent with climatic changes (Parmesan and Yohe, 2003; Parmesan, 2006). The inconsistent shifts likely reflect the different degrees to which nonclimatic factors influence species distributions (Hellmann *et al.*, 2008b). For example, local-scale patterns, species interactions, habitat requirements, or proximity to source populations may be more important than climatic conditions in determining range shifts and establishment for some species (Elliott, 2011; Matthews *et al.*, 2010; Melles *et al.*, 2011). Many factors that interact with climate change to influence species distributions make projecting climate impacts on species ranges particularly difficult.

Nonetheless, many studies have used predictive models to project the potential effects of climate change on species distributions. Most of these studies have used species distribution models (often referred to as niche models or climate-envelope models in the context of climate change) that relate current climatic patterns to current species distributions and use this relationship along with projections of future climate from general circulation models to project future species distributions (Pearson and Dawson, 2003; Guisan and Zimmermann, 2000). These projections are often consistent with the direction of observed range shifts. Bioclimatic model projections can provide useful approximations of the magnitude and location of climate-induced changes to continental biodiversity. Projections have been made for a wide array of plants and animals in most regions of the world.

Despite widespread use of bioclimatic models, there are many uncertainties associated with the projections they produce. For example, projections from bioclimatic models are sensitive to the uncertainties associated with forecasts of future climate and the type of bioclimatic model employed.

Disparate projections can be summarized using ensembles of different types of species distribution models that incorporate projections from multiple climate models (Buisson *et al.*, 2010). In addition to the uncertainties, bioclimatic models have other limitations. For example, they generally do not incorporate the influence of nonclimatic factors (e.g., species interactions, dispersal potential, or habitat requirements), the potential for species to adapt to new climatic conditions rather than move to regions of suitable climate, and the possibility that species distributions are not at equilibrium with respect to current climatic conditions (Pearson and Dawson, 2003; Yates *et al.*, 2010; Dormann, 2007). Some bioclimatic models have addressed these limitations by incorporating dispersal potential, biotic interactions, or habitat data (Carroll, 2010; Vos *et al.*, 2008; Midgley *et al.*, 2006). Process-based models further incorporate detail by including biological processes parameterized by observations or measured species physiological tolerances and may provide more accurate forecasts of species distributions (Morin *et al.*, 2008; Morin and Thuiller, 2009; La Sorte and Jetz, 2010; Morin and Lechowicz, 2008).

## Population Processes

Although projected range shifts provide a coarse view of how species will likely respond to climate change, they do not capture detailed changes that will occur at finer spatial scales. For example, climate change affects population processes such as birth and death rates, individual growth and reproductive capacity, life expectancy, immigration, and emigration. All of these processes affect short- and long-term changes in the size and age-structure of populations and determine whether populations increase, decrease, are able to establish in unoccupied regions, or go extinct. By observing population sizes and demographic parameters through time and by modeling population dynamics using observed vital rates, the authors have gained tremendous insight into climate-sensitive population processes.

Climate change affects population dynamics directly when changes in temperature, precipitation, or other climate factors alter vital rates in a population. Diverse population responses have been observed and forecasted, with some populations increasing due to climate change, others decreasing, and still others remaining essentially stable. Many insect populations, including mosquitoes and some beetles, are expected to increase in a warmer world, often because reproductive success (specifically, hatching and larva survival) is positively correlated with temperature (Morin and Comrie, 2010; Jonsson *et al.*, 2007; Estay *et al.*, 2009). Alternatively, populations of other organisms, such as tree species in western North America and polar bears in the arctic, are expected to decrease because of increased mortality rates associated with climate change (van Mantgem *et al.*, 2009; Molnar *et al.*, 2010). Because, for some species (e.g., many reptiles), the sexes of offspring are determined by temperature, changes in climate are expected to alter sex ratios, which may decrease long-term population viability (Mitchell *et al.*, 2010).

Climate change also indirectly affects population processes through interspecific interactions. Climate-sensitive dynamics in one species may lead to altered population processes of another species. For example, in alpine areas of Colorado, USA, the growing season has lengthened over the past 30 years, leading to declines in yellow-bellied marmot mortality, which triggered increases in their population sizes (Ozgul *et al.*, 2010).

Within communities and ecosystems, population-level responses to climate change vary greatly between and within species. For example, forecasted temperature increases are expected to cause rising soil temperatures in much of the world, potentially differentially affecting the longevity and dynamics of persistent soil seed banks of plants. In an arid region of Australia, some plant species showed significantly greater levels of germination after exposure to predicted increases in soil temperatures, whereas others experienced dramatic decreases in seed viability (Ooi *et al.*, 2009). Even within a species, population-level responses to climate change may differ. For example, American beaver populations are predicted to expand modestly at their northern range limits as a result of climate change, but population densities are likely to increase more dramatically in the interior portions of the beaver's range (Jarema *et al.*, 2009).

Even small alterations to vital rates due to climate change can have large consequences for population trajectories (McRae *et al.*, 2008). As computing power has increased, the capacity to model the effects of climate change on population dynamics has improved, and in recent years, studies have combined climate forecasts or bioclimate envelope models with population viability analyses and spatially explicit stochastic population models (Ooi *et al.*, 2009; Keith *et al.*, 2008; Mitchell *et al.*, 2010). Such forecasts are data and computationally intensive, but enable one to understand and better prepare for ecological impacts of climate change.

## Interspecific Interactions

Climate-change-induced shifts in ranges, phenology, and population dynamics can lead to altered interspecific interactions and the formation of novel communities. Even strongly interacting species, such as specialist pollinators and the plants they pollinate, may have large differences in their physiological tolerances, life history strategies, and dispersal abilities. Differences in sensitivities and adaptive capacities can lead to decoupling of even the strongest relationships. Species' individualistic responses to climate change make forecasting altered species' interactions enormously challenging, and scientists often combine observational or experimental studies with modeling.

Climate change affects species interactions both within and across trophic levels. Effects on plant interactions are the best documented, but recent studies suggest that climate change alters competitive interactions among animals as well and causes shifts in other interspecific relationships across trophic levels. Increasing temperature and carbon dioxide may intensify pathogen infection rates, weaken mutualisms involving plants (e.g., pollination and seed dispersal), and enhance herbivory, particularly by insects (Parmesan, 2006; Tylianakis *et al.*, 2008; Traill *et al.*, 2010). Studies predict largely negative ramifications for important ecosystem services provided by species interactions, such as natural pest control by consumers of insects, as well as the potential for increases in species coextinction rates (Traill *et al.*, 2010).

It is challenging to anticipate future effects of climate change on species interactions, but the ability to accomplish this is improving with the development of new forecasting tools and with an expanded knowledge base and data. Bioclimatic models can be fit separately for interacting species to evaluate the likelihood of altered interactions under future climates (e.g., interaction between a monophagous butterfly and its larval host plant) (Schweiger *et al.*, 2008). Bioclimatic models can also be nested, with the output for one species becoming a predictor variable for another species, to incorporate species interactions into projections of range shifts. Including these interactions is generally thought to improve explanatory and predictive power (Preston *et al.*, 2008; Sutherst *et al.*, 2007; Araújo and Luoto, 2007). Mechanistic models that explicitly incorporate species interactions can also be used to forecast range shifts (Ponti *et al.*, 2009), but these models are data intensive. Thus, observational and experimental studies are also needed to improve the understanding of species interactions and effects of climate and carbon dioxide concentrations on these interactions, particularly for mammals, amphibians, fungi, and other understudied organisms.

## Diseases and Parasites

Diseases and parasites are specific instances of interspecific interactions that will likely be affected by climate change. The impacts of climate change on terrestrial species (i.e., phenological changes, range shifts, and changes in population processes) also affect parasites, diseases, disease vectors, the susceptibility of hosts, and the interactions between all of these organisms. Therefore, climate change will both directly and indirectly affect the emergence and spread of parasites and disease (Canto *et al.*, 2009). The impacts of climate change on parasites, diseases, vectors, and hosts are individualistic, and interactions between these impacts are complex (Moller, 2010; Luck *et al.*, 2011; Lafferty, 2009; Garrett *et al.*, 2011). However, the frequency of parasite and disease outbreaks will likely increase in a changing climate (Canto *et al.*, 2009; Brooks and Hoberg, 2007). These outbreaks have the potential to negatively impact plants and wildlife, agriculture, and human health (Reid and Gamble, 2009; Luck *et al.*, 2011; Patz *et al.*, 2007; Fussel, 2008; Garrett *et al.*, 2006).

Physiological tolerances to climatic conditions often determine disease and parasite distribution and abundance. Therefore, climate change will directly impact diseases with free-living life stages and diseases that require ectothermic vectors or hosts (Mas-Coma *et al.*, 2009; Patz *et al.*, 2008; Polley and Thompson, 2009). For example, the ability for parasites or disease vectors to overwinter requires a specific range of climatic conditions (Garrett *et al.*, 2006). Also, incubation time and the number of generations per year for some vectors and parasites are sensitive to temperature and humidity, and therefore, outbreaks of diseases and parasites will be impacted by climate change (Patz *et al.*, 2008; Jaramillo *et al.*, 2009). In general, higher precipitation and temperatures correspond with a higher disease transmission rates and higher diversity of diseases (Lafferty, 2009; Froeschke *et al.*, 2010). However, the responses of parasites and diseases to climatic changes are species specific, and so the resultant impact on hosts may be positive, negative, or neutral (Garrett *et al.*, 2006). For example, for a single host species, multiple parasites responded differently to changes in different climatic variables, resulting in no change to the fitness of the host species (Moller, 2010).

Because of the individualistic responses of parasites, diseases, vectors, and hosts to climate change and the complexity of the interactions of these responses, forecasting the impact of parasites and disease is difficult. Despite these complexities, projections are important to identify regions that are most susceptible to disease emergence or parasite outbreaks to facilitate proactive responses. Process-based models are often used to forecast the response of diseases to climatic changes by modeling climatic tolerances for survival, transmission, and reproduction (Rosenthal, 2009). For example, plague levels in black-tailed prairie dogs are forecasted to decrease due to inhibited transmission from higher temperatures (Snall *et al.*, 2009). Likewise, a simulation of host–parasite dynamics forecasts reduced transmission rates from stochastic events in regions of host expansion (Phillips *et al.*, 2010).

Phenological changes will also impact disease and parasite transmission and abundance. For example, increases in the length of flying seasons of disease vectors and parasites may increase disease transmission and the spread of the disease (Canto *et al.*, 2009). Conversely, phenological changes may also reduce the impact of parasites and disease by causing mismatches with hosts. Process-based models can also forecast phenological changes and the effects of those changes on population dynamics and pathogen–host dynamics (Ogden *et al.*, 2008a).

As climates change, new regions may become climatically suitable for a parasite, disease, or disease vector. Diseases and parasites may expand into these previously unsuitable, uninhabited regions. Species distribution models have been used to project range shifts for diseases, parasites, vectors, and hosts. For example, species distribution models for a tick, *Rhipicephalus appendiculatus,* and several host species forecasted overall range reductions for the tick and hosts, but an increase in tick–host assemblages in certain regions (Olwoch *et al.*, 2009). As for all species, nonclimatic factors such as dispersal limitations, land use, and interspecific interactions may limit climate-induced range expansions (Lafferty, 2009). However, disease and parasite distributions may be even more sensitive to nonclimatic distributional determinants because of their complex interactions with vectors and hosts. Therefore, forecasts from species distribution models may not be as effective as process-based models for anticipating the impacts of climate change on parasites and disease. For parasites and diseases, in particular, host availability may influence range expansion (Lafferty, 2009; Rosenthal, 2009). For example, if parasite or disease distributions are limited by host availability, distributional shifts of host species may correspondingly cause shifts in disease and parasite distributions. Also, climate change increases the potential for host switching, which may cause disease outbreaks in previously unaffected species that may be difficult to anticipate (Brooks and Hoberg, 2007). Pest and disease control may also have a large influence on the distribution of a disease (Rosenthal, 2009). Diseases that affect humans in particular are sensitive to nonclimatic distributional determinants due to public health programs that are often influenced by socioeconomic distributions (Rosenthal, 2009). The extensive influence of nonclimatic factors on the distributions of diseases and parasites may overwhelm the impact of climate change, making impacts somewhat difficult to forecast.

## Interactions with Other Stressors

Climate change will not affect species in a vacuum, but instead will interact with other factors that currently affect population dynamics or species distributions. These other factors include, but are not limited to, invasive species, land-use change, disturbance, and human responses to climate change.

### *Invasive Species*

Invasive species are also experiencing changes in phenology and distributions, which may exacerbate the threats of climate change to native species. Climatic changes are likely to result in increases in invasive species' survival, abundance, and range expansions. Experiments and field observations provide evidence of the tendency for invasive species to outcompete native species in a changing climate (Verlinden and Nijs, 2010; Willis *et al.*, 2010). First, invasive species have a higher propensity than native species to adjust their phenology in accordance with climatic changes. The more adaptable phenologies of invasive species facilitate community invasions and also lead to increases in the abundance of invasive species (Willis *et al.*, 2010). Moreover, characteristics common to invasive species such as high dispersal abilities, high growth rates, short generation times, and broad climatic tolerances facilitate rapid range expansion in accordance with the rapid changes in climatic conditions (Schweiger *et al.*, 2010; Hellmann *et al.*, 2008a). Bioclimatic models can forecast the extent of a species' invasive potential in a changing climate by projecting the distribution of suitable climate for the invader. Forecasts of potential invasions from climate-change-induced expansions comprise most of the recent research on the interaction of invasive species and climate change. Generally, these models predict expansions of the invaders' ranges (Bradley *et al.*, 2010; Jarnevich and Stohlgren, 2009). However, in regions where they anticipate contractions, forecasts can provide useful guidance for restoration of sites that are no longer suitable for an existing invader (Bradley and Wilcove, 2009). Incorporating invasive ranges into bioclimatic models may also be useful for improving the forecasts of species distributions by more accurately approximating fundamental climatic niches (Beaumont *et al.*, 2009).

Climate-change-induced range shifts of native species may challenge the traditional definitions of nonnative and invasive species as ranges expand beyond species' historical distributions. Previously noninvasive species have the potential to become invasive in a new region without the biological controls provided by interspecies interactions present in the previous community (Hellmann *et al.*, 2008a). Bioclimatic models do not predict these changes in fitness or species interactions and so may underestimate the potential for ecosystem invasions from previously noninvasive species.

### *Land-Use Change*

Changes in land use, and the corresponding habitat destruction, are currently the greatest threats to biodiversity (Hoffmann *et al.*, 2010; Dawson *et al.*, 2011). The interaction between climate change and land use may exacerbate the impacts of both stressors to flora and fauna. Land use may limit species' range expansions by inhibiting population establishment or impeding movement to climatically suitable regions (Feeley and Silman, 2010). This inability to realize range expansions may result in reductions in range size and decreases in species richness. Climate projections and associated response models can be used to assess these potential interactions and compounding impacts. For example, a process-based dynamic global ecosystem model forecasted a shift in the climatic conditions that are associated with high species richness in northern South America from less impacted to highly modified landscapes that cannot support as many species, resulting in a reduction in overall richness (Higgins, 2007).

Not only will land use inhibit range expansions, but it may also cause distributional shifts (Hockey *et al.*, 2011; Gehrig-Fasel *et al.*, 2007). These range shifts either augment climate-induced shifts or result in shifts inconsistent with the direction of climatic changes. Climate projections can also be coupled with land-use projections to anticipate species responses to these combined threats. For example, in Switzerland, the broad-scale changes forecasted in the distributions of nonvascular plants were attributed to climate change, whereas more local scale changes were attributed to land-use change (Nobis *et al.*, 2009). An individual-based population model anticipated that projected land-use changes will have a larger impact on habitat quality than climate change, but that climate change is still likely to impact the population dynamics of two bird species in the Willamette National Forest (McRae *et al.*, 2008).

Land use may also act as an additional driver of phenological advancement and may further exacerbate the impacts associated with phenological changes (Neil *et al.*, 2010). For example, urbanization may create warmer microclimates resulting in further advancement of phenology (Neil *et al.*, 2010). Together, land-use change and climate change also lead to increases in the prevalence of invasive species and diseases, further challenging floral and faunal communities (Crowl *et al.*, 2008; Patz *et al.*, 2008). Modeling approaches that anticipate impacts will be important for proactive management to address these potential compounding threats.

### *Disturbance*

Climate change has the potential to alter the frequency and severity of disturbances, such as fire, resulting changes in ecosystem structure and/or function. Climate change has already altered fire regimes through increases in fire severity and area burned, and these impacts are projected to increase in the future (Littell *et al.*, 2009; Marlon *et al.*, 2009; Nitschke and Innes, 2008; Podur and Wotton, 2010). Increases in fire severity alter community composition through the loss of nonvascular plants, shrubs, and drought-sensitive species and the rapid species establishment that succeeds severe burns (Colombaroli *et al.*, 2007; Bernhardt *et al.*, 2011). Climatic changes may also increase the fire susceptibility of communities that have historically lacked fire regimes. Ignition in these newly susceptible regions will further alter community composition (Malhi *et al.*, 2009).

Many studies have forecasted changes in fire severity and the area burned. These projections are significantly different from historical time-series simulations (Keane *et al.*, 2008) and generally include longer fire seasons, increases in fire severity, shifts toward full crown fires, and increases in the area burned (Podur and Wotton, 2010; Nitschke and Innes, 2008; Malevsky-Malevich *et al.*, 2008). However, far fewer studies forecast the impacts of these fire-regime changes on species and community composition.

### *The Human Response to Changes in Ecosystem Services*

Through impacts on species, communities, and ecosystems, climate change will alter the goods and services provided by Earth's ecosystems. Ecosystem services include a wide array of benefits that people derive from ecosystems including provisioning, regulating, cultural, and supporting services. Provisioning services are those that deliver products that humans use (e.g., water, food, fiber for clothes, and shelter). Regulating services are those that control the states and rates of physical and biotic systems and processes in ways that are beneficial to humans (e.g., the reduction of storm-surge damage by mangrove forests, flood control by riparian systems, and carbon sequestration and storage by plants). Cultural services increase societal and spiritual well-being (e.g., the provision of recreational amenities, spiritual experiences, esthetics, and human health). Supporting services are those that assist in the provision of all other services such as nutrient and water cycling, pollination, and nitrogen fixation.

There are many ways in which climate change will alter the quantity or quality of the four different types of services. For example, shifts in species distributions have the potential to directly affect the provision of many food resources, particularly for human communities that rely on wild-caught foods. Climate change will also affect regulating services such as the ability to grow specific crops in particular locations (Lobell and Asner, 2003; Lobell and Field, 2007; Battisti and Naylor, 2009) and the quantity and quality of water for drinking and irrigation (Vörösmarty *et al.*, 2000). Changes in phenology, pollinator communities, soil microbial communities, the distribution of pest and pathogens, and invasive species all have the potential to alter supporting services for food production. Changes in microbial communities also have the potential to alter nutrient cycling, water purification, and timber and other fiber production.

Understanding how ecosystems services will change in the future and how humans will respond will be a critical step in developing adaptation strategies for species and systems. Crop failure, water shortages, and sea-level rise will force human migrations and likely result in conflicts between humans and terrestrial species, particularly in developing countries. These migrations and conflicts will further displace some terrestrial species and potentially provide opportunities for others. Shifts in the modes of energy production also have the potential to negatively impact species as solar arrays, wind farms, and biomass production replace oil and gas extraction. Efforts to increase carbon sequestration, however, have the potential to benefit species depending on the approach taken.

Studies have begun to examine the potential effects of climate change on specific ecosystem services; however, few studies have attempted to evaluate the impacts of climate change on suites of ecosystem services (Hayhoe *et al.*, 2004; Metzger *et al.*, 2008; Schröter *et al.*, 2005; Alcamo *et al.*, 2005). Many of the methods that are applicable to projecting changes in ecosystem services are those that can be used to assess the potential effects of climate change on species and ecological systems. In addition to these approaches, methods for quantifying the services themselves will also be needed. Many models have been devised for evaluating ecosystem services (Kareiva *et al.*, 2011), and some of these have been coupled with climate projections to investigate the impacts of climate change on these services (Lawler *et al.*, 2011). Estimating the human response to these changes in services requires going beyond the ecosystem service model projections and forecasting human migrations, land-use changes, water use, and other human actions. These predictions can, like the projections of ecological responses, be derived from predictive models or be based on historic patterns or the results of surveys and other socioeconomic studies.

## Adaptation

There are two types of actions that humans can take to reduce the impacts of climate change. Mitigation actions reduce the amount that the climate will change. Such actions include approaches for reducing greenhouse gas emissions and sequestering atmospheric carbon dioxide. Adaptation actions are those that reduce the impact of a given magnitude of climate change and include approaches such as protecting more land, restoring riparian areas to reduce stream temperatures, and moving species to more suitable climates. There are several general concepts that have guided the development of adaptation strategies. These are discussed in the section, General Concepts and Principles, below. This section is followed by sections describing specific Adaptation Strategies, Challenges to Adaptation, and the co-benefits of adaptation (in Multidimensional Strategies).

### General Concepts and Principles

Many of the commonly recommended climate-change adaptation strategies for species and ecological systems tend to be general concepts for altering the way species and systems are managed. These concepts include assessing vulnerability, managing for resistance and resilience, planning at broader spatial scales, increasing cooperation and coordination in planning and management, and employing adaptive management and triage when necessary. These general concepts are discussed briefly.

#### *Vulnerability*

Climate-change adaptation is deeply tied to the concept of vulnerability – the extent to which a species, an ecosystem, or an area is likely to be harmed as a result of climate change and associated stresses (Brooke, 2008). Vulnerability can be defined as having three components: sensitivity, exposure, and adaptive capacity (Dawson *et al.*, 2011). Sensitivity refers to innate characteristics of an organism or ecosystem (e.g., tolerance to changes in temperature) that predispose it to being more or less susceptible to climate change. Exposure refers to the amount of change either in climate or in climate-driven factors that a species or system will face. Adaptive capacity is a measure of the ability of a species or system to respond in a way that reduces the impacts of, or to takes advantage of, climate change. Vulnerability assessments inform adaptation planning by documenting aspects of all three of these components of vulnerability and using them to identify which species or systems will be affected by projected climate changes and the causes of those impacts Glick *et al.* (2011).

### Resistance, Resilience, and Fostering Change

There are three general approaches to managing systems in the face of climate change. One can attempt to manage a system to resist change, to make it resilient to climate change, or to foster change to a new state. Much discussion has focused on managing for resilience. Resilience can be defined in several ways. Here, resilience is defined as the ability of a species or system to return to its current state following a perturbation (e.g., Holling, 1973). Systems that are resilient to climate change will be able to maintain ecosystem functions and processes and avoid a transition to a new state as climates change. Managing for resilience is an attractive concept, because, if successful, it allows continued delivery of ecosystem services and, possibly, the persistence of plant and animal populations.

Many of the other general concepts as well as most of the more specific adaptation strategies focus on increasing resilience. For example, reducing other (nonclimatic) threats, increasing genetic diversity, and restoring riparian vegetation are all approaches that will likely increase the resilience of a species or system in a given place. Removing barriers to inland migration of coastal species is also a potential strategy for increasing the resilience of a species, albeit by increasing the adaptive capacity of species to address change.

Given the magnitude of change that is projected for the coming century, it may be impossible to foster resilience in many systems. Managing these systems may require promoting change to a new state. Promoting change in human-dominated systems will likely be more straightforward (e.g., planting new crops) than doing so in more natural systems. Strategies for fostering change include assisted colonization (see below), shifting management efforts from one species to another and more specifically promoting newly arriving species. The outcomes of these more aggressive and forward-looking strategies will be more uncertain and their implementation (as is already evident with assisted colonization, Ricciardi and Simberloff, 2009) will be more controversial.

### Spatial and temporal scales

Climate change is a global phenomenon that will result in long-term changes in ecological systems. The spatial and temporal scales of the changes one is likely to see far exceed the scale of the traditional 1 $m^2$ ecological sample plot and the time-span of an ecological study. More importantly, these changes exceed the spatial and temporal scales over which most planning and management occur. Managing for species and systems in a changing climate will require taking a broader spatial and temporal perspective (Welch, 2005; CCSP, 2008). Developing climate-change adaptation strategies for species will require planning at regional and, perhaps in some instances, continental scales (Hannah, 2010). Because ecological systems will be undergoing relatively rapid changes for the foreseeable future, managers will have to manage for moving targets. The whole concept of "restoration" must be reconsidered (Harris *et al.*, 2006). Returning ecosystems to a previous state (e.g., before human settlement) with a complement of species that were historically native to the site might be counterproductive in a changing climate.

Similarly, the time frame for planning and management actions will, in many cases, need to shift to address climate change. Planning horizons have traditionally been relatively short – for example, 3- to 5-year plans. Planning in such small increments is likely to result in short-sighted management strategies that are incapable of addressing climate change. Managers and scientists need to strike a balance in terms of the temporal and spatial scales over which climate impacts are projected and the scales at which strategies and plans are developed. Many of the ecological climate-impact forecasts are for periods of 50–100 years in the future. Although these projections will be useful for developing management strategies, mangers will also need 10- and 20-year projections.

### Cooperation and Coordination

Given the broad spatial scales that will need to be considered to address climate change, managers, planners, and policy makers will need to work together and to coordinate efforts across jurisdictions and traditional management units (Kareiva *et al.*, 2008). This will mean developing regional instead of local efforts in which strategies are designed to reach across state, province, or country borders. It will mean collaboration across different governmental agencies that are currently focused on specific systems (atmospheric, marine, freshwater, and terrestrial). It will also mean increasing cooperation among different types of groups such as nongovernmental organizations, local and regional governments, citizen groups, and industry. The US Climate Change Science Program (CCSP) is one such organization that reaches across federal agencies. Other regional and national efforts have been put in place in other parts of the world, but such efforts will need to be increased to address climate change.

### Managing for Process Over Composition

Because changes in climate will drive species range shifts resulting in new communities, it will be exceedingly difficult to manage for specific assemblages of species. Many have suggested that such changes will necessitate a shift from managing for species and communities to managing for ecosystem processes and shifting baselines (Harris *et al.*, 2006; Heller and Zavaleta, 2009; Hobbs *et al.*, 2009). In many systems, managing for ecosystem function may mean taking a forward-looking approach in which new species are planted or introduced into a system. As discussed below in the context of assisted colonization, these more manipulative approaches that tend toward engineering ecosystems and moving species have raised significant concerns and debates about the unintended consequences of such actions.

### *Triage*

Many species and systems will be highly vulnerable to climate change. Given the relative scarcity of funds for conservation, it will be impossible to address the needs of all species. Thus, conservation planners and managers will have to make difficult decisions about how to allocate limited funds. They will likely have to choose which populations and species to try to save and which to let go extinct. Triage is one approach to making such difficult prioritizations.

Triage is a medical ranking system developed for the treatment of patients in emergency situations. Traditionally, the system has had four levels based on the severity of the injuries and the likelihood that the patient will survive. The levels are generally deceased or expectant, critical, severe, and minor. A similar system can be applied to species or populations at risk of extinction in the face of climate change (Lawler, 2009). In such a system, some species would be classified as likely to experience such large changes that management actions will do little to prevent their decline or loss. Other species would be deemed as critically threatened by climate change, but their decline or extinction could be prevented by immediate and intense management efforts. A third class of species would be threatened by climate change but would not be at risk of extinction in the short term, and thus management effort could wait. A final class of species would face relatively minor threats from climate change and could be monitored over time and addressed later if necessary. Although there are both ecological and ethical considerations that make triage unpopular (Kareiva and Levin, 2003), such a system will undoubtedly become necessary as climates change and ecological systems respond.

### *Adaptive Management*

Adaptive management is an iterative process of management and monitoring in which management actions are treated as experiments (Holling, 1978; Walters and Hilborn, 1978). The outcomes of these experiments are used to inform the next round of management actions, which are again treated as experiments. Adaptive management was conceived of for managing uncertain systems, making it potentially a highly useful approach to deal with climate change (Arvai *et al.*, 2006). To address climate change, adaptive management approaches will have four basic steps that will be iteratively repeated (Kareiva *et al.*, 2008). The first step will involve assessing the potential impacts of climate change on the system in question. In the second step, management actions, in the form of experiments with testable hypotheses or predictions, will be designed to address one or more of these potential impacts. The third step involves monitoring the system for climatic changes and system responses. Finally, the results of the monitoring can be used to evaluate the effectiveness of the management actions and to redesign them as necessary before the four steps are repeated.

## Adaptation Strategies

Climate-change adaptation strategies are practices and adjustments that enhance resilience and/or reduce vulnerability to changes in climate (IPCC, 2007a). These strategies have been implemented across the globe on a limited but increasing basis, in both developed (Krysanova *et al.*, 2010; Olesen *et al.*, 2011; Tompkins *et al.*, 2010; Wheeler, 2008) and developing countries (Krysanova *et al.*, 2010; Mertz *et al.*, 2009; Ziervogel and Zermoglio, 2009). The following section describes some of the adaptation strategies that have been proposed for protecting terrestrial species in a changing climate.

### *Protected Areas: Reserve Selection and Design*

By providing species with refuge from many threats, protected areas have the potential to increase the resilience of species and populations to climate change (Hunter *et al.*, 2010). However, climate change brings into question the ability of current protected lands to provide for the biodiversity of the future. Typically, reserve boundaries are static and reserve networks are designed based on current biodiversity. As species' ranges shift with a changing climate, some species may lose protection as their ranges shift out of reserve boundaries, whereas others may move into reserves (Peters and Darling, 1985). Reserves across the globe are anticipated to experience changes in biodiversity composition, and several species may lose protection entirely from the current reserve network (Araújo *et al.*, 2004; Hole *et al.*, 2009). One adaptation response that aims to provide protection for anticipated climate-induced changes in species distributions has been to augment the reserve network by adding reserves to increase the total area protected across a landscape.

Several general rules of thumb have been proposed for addressing climate change in the reserve selection (i.e., the placement of new reserves) and reserve design (i.e., the size and shape of reserves) processes. Most simply, many have suggested increasing the total area protected and increasing the size of existing reserves. All else being equal, larger reserves will be more likely to maintain populations of species as climates change by providing the space to facilitate within-reserve range shifts. Thus, designating larger reserves or designating buffer zones around reserves may help to protect more species for longer periods of time in a changing climate (Peters and Darling, 1985). Similarly, reserves that span strong environmental gradients will also provide more opportunities for within-reserve range shifts by providing future niches at different altitudes as the climate changes. Strategies for the placement of new reserves include placing reserves at the elevational or poleward range limit of key species (Peters and Darling, 1985), at major transitions between vegetation formations (Halpin, 1997) or at the core of species environmental distributions (Araújo *et al.*, 2004). Yet another simple suggestion involves increasing the redundancy in the reserve system. Protecting the same species in multiple places provides multiple opportunities for the species to weather or adapt to climate change.

Others have suggested more sophisticated methods for identifying the best places for new protected areas to address climate change. For example, projected shifts in species distributions can be used to identify areas that are likely to protect species today as well as into the future under multiple climate-change scenarios (Hannah *et al.*, 2007; Vos *et al.*, 2008). The increase in specificity potentially makes this approach more effective for the targeted species; however, it incorporates higher levels of uncertainty inherent in forecasting future climatic changes and the biotic responses to those changes. For example, the most-often-applied approach for forecasting species range shifts, species distribution or niche modeling, is better suited to describe general patterns and trends in range shifts than to identify particular locations for protecting specific species in the future (Pearson and Dawson, 2003).

Another approach to locate reserves to address climate change involves selecting areas that protect the underlying environmental gradients that largely determine patterns of biodiversity at broader scales, but that will likely remain stable as the climate changes. It has been argued that protecting these underlying gradients essentially protects the stage on which biodiversity will play out as climates change. Some proposed strategies based on abiotic features focus on selecting sites that span elevational gradients or that represent heterogeneity in soils (Peters and Darling, 1985). Other have stressed geologic variability in a reserve network (Anderson and Ferree, 2010), preserving a range of current climatic conditions – with the assumption that future climates may change, but that many climatic gradients will be preserved (Pyke and Fischer, 2005) – and conserving the regional diversity of land facets, or unique combinations of abiotic conditions (i.e., topographic and edaphic features) (Beier and Brost, 2010). These strategies seek to maintain the elements of the landscape that are responsible for the distribution of regional biodiversity, may be more effective due to more specificity in reserve placement, and are robust to the uncertainties of forecasts.

Other abiotic-based strategies target climate conditions by placing reserves in regions projected to be climate refugia. Planners refer to climate refugia both as areas that are projected to experience minimal climatic changes and as areas projected to have cooler microclimates (Hansen *et al.*, 2010; Shoo *et al.*, 2011; Saxon *et al.*, 2005). The former aims to reduce the potential changes in species composition of new reserves so that these reserves will be more effective over a longer period of time for currently protected species. The latter aims to reduce the distance necessary for distributional shifts by locally protecting cooler microclimates. Locally cooler microclimates may occur at slightly higher elevations or be in areas with more vegetative cover or potential for vegetative cover. Although these strategies may depend on uncertain climate projections, they avoid the compounding uncertainty of using climate projections to forecast biotic responses and still incorporate specificity into the planning process.

### Connectivity

Range shifts have occurred in the past as species have responded to historical changes in climate. However, during these periods of historical climate change, species movements were not hindered by anthropogenic barriers. Fragmentation of habitat, roads, and other barriers can inhibit species movement or survival in regions of or between newly suitable climates. Not surprisingly, increasing landscape connectivity is the most commonly recommended adaptation approach for addressing climate impacts on biodiversity (Heller and Zavaleta, 2009).

Until recently, suggested strategies for improving connectivity to address climate change have been somewhat general – for example, placing new reserves between existing reserves, creating a system of stepping stone reserves, or adding reserves in proximity to existing reserves. Recently, studies have highlighted more sophisticated approaches to connecting landscapes to address climate change. One such approach uses climate projections to orient corridors and expand existing reserves in the direction of anticipated climatic changes (Ackerly *et al.*, 2010). Other approaches involve using projected shifts in species distributions to identify potential routes that species would need to take to move from currently suitable climates to places where climates will likely be suitable in the future (Williams *et al.*, 2005; Rose and Burton, 2009). Beier and Brost (2010) recommend using abiotic elements or land facets (described above) to define corridors. Similar to the multiple reserve placement approaches, these connectivity approaches vary in the level of uncertainty in the data, models, and model projections that they draw upon.

Although it will be important to identify potential movement corridors, increasing the permeability of the landscape in general will also be critical (Franklin and Lindenmayer, 2009). It may be possible to manage lands to facilitate species' movements in response to climate change. For example, selective harvest or retention cuts, tree planting, and rotational grazing may provide habitat to facilitate range expansions (Manning *et al.*, 2009; Kohm and Franklin, 1997). It is possible to prioritize areas for these incentives and management actions using approaches similar to those discussed above for the placement of reserves or corridors.

### Species- and Place-Specific Approaches

The adaptation approaches discussed above tend to be general concepts or broad-scale actions (reserve selection and promotion of landscape connectivity). Despite the fact that climate change is a global issue and landscape-level actions are therefore necessary, species- and place-specific approaches will also likely be critical components of climate-change adaptation. Species-specific adaptation strategies aimed at preventing extinction of a particular organism may be appropriate for threatened and endangered species for which legal frameworks, such as the US Endangered Species Act and the International Union for Conservation of Nature (IUCN) Red List, may require species-specific protection and for organisms of economic importance to humans. Place-based approaches, such as efforts focused on a particular park or preserve or within a particular city, are important because adaptation strategies are likely to be implemented at local scales, by the private and public landowners and managers. Proactive management can address the vulnerability of an area or a species by reducing exposure through the manipulation of microclimates, by reducing sensitivity, and by increasing adaptive capacity.

There are several ways in which the degree of local exposure to climate change can be altered. For example, species-based approaches may include supplemental watering of key plant species in drought years (e.g., Pavlik *et al.*, 2002) and altering microclimates of artificial nest boxes for rare birds by painting boxes white or locating them on north-exposed slopes (Catry *et al.*, 2011). Place-based approaches can rely on microclimatic variations that provide refugia from large-scale changes in climate (Mosblech *et al.*, 2011). Place-based approaches to reduce exposure may therefore include protection of these natural refugia, as well as planting trees and other vegetation to provide shade and reduce temperatures (Wilby *et al.*, 1998; Wilby and Perry, 2006). These relatively fine scale adaptation actions are often successful, at least in the short term, but may become increasingly expensive, time consuming, and impractical as climate-change progresses.

Adaptation strategies can also address the vulnerability of an area or a species by reducing sensitivity to the effects of climate change. Diverse systems are generally less sensitive to disturbances (Kareiva *et al.*, 2008; Fargione and Tilman, 2005; Schindler *et al.*, 2010). This pattern is true for genetic diversity within a population of a single species (Schindler *et al.*, 2010), as well as for species richness at the ecosystem level (Chapin *et al.*, 2000). Thus, promoting and protecting diversity at multiple levels, from within a species or a population to across different species and functional groups in an ecosystem, is an important adaptation strategy (Glick *et al.*, 2009).

Adaptation strategies can address vulnerability of an area or a species by reducing sensitivity to climate change or by strengthening its adaptive capacity to respond to the effects of climate change. Other stressors, such as land use, invasive species, pathogens, fragmentation, and pollutants, interact with climate change to further harm species and natural systems (Schweiger *et al.*, 2010; Walther, 2010). Reducing these other stressors can increase adaptive capacity and decrease sensitivity to climate change (Glick *et al.*, 2009). Species-specific approaches include reducing harvest levels of focal organisms, limiting their exposure to pollutants and pathogens, reducing habitat loss, and improving connectivity between populations through corridors (Heller and Zavaleta, 2009; Glick *et al.*, 2009). Worldwide conservation efforts have already reduced species' extinctions, particularly by mitigating threats from invasive species on birds and mammals, but efforts need to be augmented in order to abate many substantial threats to global diversity (Hoffmann *et al.*, 2010).

Assisted colonization – the translocation of species outside their native range to facilitate movement in response to climate change – is another strategy for increasing the adaptive capacity of a species. Assisted colonization may be most appropriate in cases in which current species' ranges become inhospitable with climate change and connectivity to suitable regions is severely limited. This approach is controversial because of the potential for negative, ecological, evolutionary, and economic impacts, as well as ethical concerns (Ricciardi and Simberloff, 2009; Sax *et al.*, 2009). Some potentially less controversial strategies include planting climate-resistant species or ecotypes (Glick *et al.*, 2009) and establishing ''neo-native forests'' in restoration efforts, that is, planting species where they were in the past, but are not found currently (Millar *et al.*, 2007). Many current restoration and forestry practices adhere to strict rules about using only ''local'' species and ecotypes. To prepare for climate change, one may need to broaden the genetic and species diversity used in restoration and forestry (Glick *et al.*, 2009). In some cases, even aggressive strategies such as assisted colonization may fail as climate change and other stresses threaten the existence of rare species. These extreme cases will require *ex situ* conservation strategies, including seed banking and captive breeding to ensure the long-term survival of the species.

Protected areas, corridors for movement, and assisted colonization may all help species track changes in climate. However, given the magnitude of projected changes, these measures may be insufficient. It may be necessary to implement policies that facilitate species movements. Such policies may prohibit the destruction of habitat or removal of species in places through which those particular species will likely need to move in response to climate change (Kostyack *et al.*, 2011).

## Challenges to Developing Successful Adaptation Strategies

There are several challenges to adaptation planning and implementation. One of the most frequently mentioned challenges to developing climate-change adaptation strategies is the lack of certainty about future climatic conditions. Although climate-change projections and projected climate impacts are necessarily uncertain, some projections are less uncertain than others and many projections can be used to inform the development of adaptation strategies. In general, projected changes in temperature are less uncertain than projected changes in precipitation and projections for the near-term are less uncertain than projections for the more distant future (IPCC, 2007b). Projected climate impacts on terrestrial species will necessarily be more uncertain than climate-change projections as they generally incorporate the uncertainties of climate models and the additional uncertainties about how species or habitats will respond to climate change and/or the uncertainty associated with the modeling approaches used to forecast those responses (Thuiller, 2004).

A second, often-cited challenge to developing adaptation strategies is the lack of projected climatic changes at a spatial resolution that is meaningful for management. The general circulation models that have been used to project changes in climate have, to date, generated projections at sales of degrees of latitude and longitude (IPCC, 2007b). These projections can be downscaled to finer resolutions; however, there are uncertainties associated with downscaling process (Dettinger, 2005; Wilby *et al.*, 1998). Despite the additional uncertainties, downscaled projections are important for understanding how climatic changes may manifest at finer scales. Downscaled data sets are currently available for many regions of the globe, and tools have been developed that make those data sets readily accessible (Girvetz *et al.*, 2009).

A third limitation to developing adaptation strategies is the general lack of information on species-specific responses to climate. Responses to interacting climate variables vary greatly across and within species, and for many terrestrial plants and animals, the relationship between climate variables and performance (i.e., growth, survival, and reproduction) is unknown (Parmesan, 2006). Climate-change effects on species are further complicated by their interactions with biotic factors, such as competition, predation, mutualisms, and other stressors, such as land use, invasive species, pathogens, and pollutants (Schweiger *et al.*, 2010; Walther, 2010). Thus, for many species, an important first step for climate-change adaption is simply to improve the understanding of responses to climate change, including physiological, behavioral, and demographic responses (Heller and Zavaleta, 2009)

Planning can be difficult in the face of these uncertainties, and currently implemented adaptation strategies are limited in scope and are insufficient to fully address climate-change impacts (Wheeler, 2008; Reyer *et al.*, 2009). One of the primary concerns expressed by land and resource mangers is a lack of "downscaled" studies on which to base their decisions, in terms of both climate projections and species responses (Glick *et al.*, 2009). However, there have been significant advances in model development at regional scales. As one's knowledge base and expertise grow, a key challenge is to improve communication and cooperation across the many groups and individuals involved in developing climate-change adaptation strategies. Species- and place-specific approaches are practical, because of existing legal, ownership, and management frameworks. Nonetheless, these approaches will be far more effective if there is substantial cooperation and communication within and between groups implementing climate-change adaptation strategies.

**Table 1** Example approaches for anticipating and adapting to climate impacts on terrestrial species

| *Impacts* | *Anticipating impacts* | *Adaptation strategies* |
|---|---|---|
| **Phenology** | | |
| Shift in grape flowering and ripening times in montane Australia (Caffarra and Eccel, 2011) | • Project changes in temperature and precipitation<br>• Apply phenological models of budburst, flowering, and fruit ripening | • Alter grape varieties grown<br>• Focus on high elevation areas, where climate may become more suitable |
| **Range shifts** | | |
| Shift in the distribution of wolverine in the US | • Project changes in snowpack<br>• Apply species distribution models<br>• Map historical ranges and climatic conditions | • Enhance connectivity both northward in latitude and upward in elevation |
| **Population processes** | | |
| Shift to male-biased sex ratios of tuatara reptiles in New Zealand (Mitchell *et al.*, 2010) | • Conduct population viability analysis under different sex ratios | • Use *ex situ* techniques to increase females<br>• Translocate populations to cooler environments or sites with more microclimate complexity |
| **Interspecific interactions** | | |
| Spatial mismatch of a monophagous butterfly (*Boloria titania*) and its larval host plant (*Polygonum bistorta*) (Schweiger *et al.*, 2008) | • Project changes in monthly temperature<br>• Apply species distribution models for two interacting species<br>• Map future ranges of two species | • Increase likelihood of plant dispersal by enhancing connectivity between habitat patches<br>• Facilitate migration of host plant through habitat restoration or planting efforts |
| **Diseases and parasites** | | |
| Change in the prevalence of East Coast Fever (ECF) in sub-Saharan Africa | • Project changes in distribution of a tick and 10 of its host species<br>• Assess the probability of occurrences of tick–host assemblages<br>• Apply dilution effect model to determine potential ECF transmission | • Regulate cattle movement to reduce interaction between cattle and wild host species |
| **Interactions with other stressors** | | |
| Impact of multiple stressors on two bird species with varying habitat requirements | • Develop spatially explicit individual-based models<br>• Apply projected changes in land use<br>• Apply projected changes in climate | • Evaluate and implement management strategies that increase population viability |

### Multidimensional Strategies (Co-benefits)

Climate change will have profound effects on many human populations (IPCC, 2007a). These effects include water shortages, crop reductions, and failures resulting in malnutrition, displacement due to sea-level rise, emerging diseases, and armed conflict (Costello *et al.*, 2009). Humans will develop adaptation strategies to reduce these impacts. Dams will be built to store water; more water will be extracted from streams and rivers for agriculture, drinking, and manufacturing; new areas will be cultivated; migrations will occur and settled areas will expand; and wetlands will be drained and pesticides applied to reduce crop pests and disease vectors. Many of these adaptation strategies will have negative consequences for nonhuman terrestrial species. Conversely, some of these strategies can be designed to benefit nonhuman terrestrial species.

Co-benefits can be defined as the positive effects that an adaptation strategy designed to address a specific human need has on nonhuman species, communities, or ecosystems, or conversely the positive effects on human well-being of adaptation strategies designed to help nonhuman species and systems adapt to climate change. Co-benefits have largely been described for mitigation strategies that, in addition to reducing greenhouse gas emissions, benefit human health (Haines *et al.*, 2007; Jack and Kinney, 2010). Such co-benefits of adaptation strategies have not been as well documented, but these win–win outcomes will likely arise in many instances.

There are clear co-benefits for human health and well-being that are likely to result from adaptation strategies that restore coastal habitats, riparian areas, and flood plains. Removing sea walls, restoring mangrove forests and dune systems, and protecting barrier beaches are all adaptation strategies that will increase the resilience of coastal plant and animal communities to sea-level rise and storm surges. These same strategies, if well designed and well sited, have the potential to protect human communities from these threats as well. Conversely, addressing these threats to humans by building sea walls will not offer the co-benefit to nonhuman species and systems. As a second example of a co-benefit, riparian restoration has the potential to reduce stream temperatures through shading and may also increase water quality and water storage for human use.

To develop strategies that maximally benefit both nonhuman and human systems and communities, it will be necessary to develop approaches for evaluating and comparing co-benefits. As of yet, little work has been done in this area, in part because it involves measuring and weighing disparate outcomes and values and because it involves collaboration and coordination across diverse disciplines. Nonetheless, such comparative metrics and analyses will be quite useful for developing strategies and prioritizing among them.

## Conclusions

Addressing climate-change impacts on terrestrial species will require at least a basic understanding of how climate change will affect species. Much is already known about climate effects on phenologies, distributions, populations, interspecific interactions, and diseases and pathogens. Although there are significant gaps in the knowledge of these effects, detailed studies of potential climate impacts on specific species are not likely to provide managers and policy makers with the most critical information for developing adaptation strategies for terrestrial species. On the contrary, research focused on developing actionable adaptation strategies from the many general concepts and basic principles that have been proposed for addressing climate change has the potential to inform the management of a wide range of species and systems. For example, research focused on approaches to adaptive management, refining triage systems, connecting landscapes to facilitate range shifts, and measuring and valuing the co-benefits of adaptation strategies for human and nature systems will be critical components of a research agenda for addressing climate impacts on terrestrial species and systems (**Table 1**).

*See also*: Climate Change and Ecology, Synergism of. Climate Change and Wild Species. Climate, Effects of. Comparing Extinction Rates: Past, Present, and Future. Conservation Efforts, Contemporary. Evolution in Response to Climate Change. Landscape Corridors. Latitudinal and Elevational Range Shifts Under Contemporary Climate Change. Mammals, Conservation Efforts for. Phenological Shifts in Animals Under Contemporary Climate Change. Plant Phenology Changes and Climate Change. Species Distribution Modeling. Wildlife Management

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