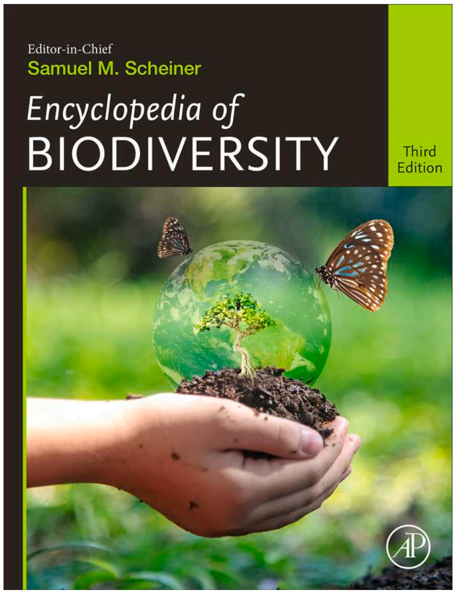

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Climate Change: Anticipating and Adapting to the Impacts on Terrestrial Species

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Abstract

Addressing the impacts of climate change on terrestrial species requires knowledge of how climates will change, how species will respond, and understanding the scope of actions that can be taken to help species and ecosystems adapt. Research in recent years has advanced knowledge of how species are being impacted by changing climatic conditions, such as drought, fire, and sea-level rise. Documented responses include, for example, shifts in phenologies, distributions, population dynamics, interspecific interactions, and disease dynamics. Many management strategies have been proposed for addressing these changes and predicted impacts, including general principles such as practicing adaptive management, fostering resilience and facilitation transformation, increasing landscape connectivity, and increasing the extent of reserve networks. Many more system- and species-specific adaptation management actions have also been developed and implemented in a diversity of landscapes and ecosystems to address the increasing impacts of climate change on biodiversity.

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Glossary

Adaptation actions that aim to prepare for or adjust to the current impacts of climate change as well as the expected impacts in the future.

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.

Climate refugia areas that will, as the climate changes, continue to have suitable climatic conditions for species that are currently there or that exist in the surrounding landscape.

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 recurring ecological events.

Resistance the ability of a system or species to remain largely unchanged in the face of climate change.

Resilience the ability of a system or species to return to its initial condition after perturbation by climate change.

Transformation allowing and/or facilitating transition to new conditions.

Key Points

- Climate change is affecting species and ecosystems in myriad ways.
- In addition to the more direct effects of increasing temperatures and changes in precipitation patterns, climate-driven changes in extreme events, fire regimes, and sea level are also having profound impacts.
- Climate change is interacting with other stressors to biodiversity including land-use change and invasive species as well as driving a host of human responses to climate change that can have additional impacts.
- Anticipating future climate impacts generally involves lessons learned from observations, experiments, and forecasting using a combination of empirical and mechanistic models.
- In general, conservation of biodiversity in a changing climate requires understanding vulnerability, managing for process over composition, and embracing adaptive management.
- Adaptation approaches for species and ecosystems include those that focus on resistance, resilience, and fostering transitions.

Introduction

Species and ecosystems are significantly impacted by climate change. Recent climatic changes have resulted in clear shifts in species distributions and the timing of ecological events (Parmesan, 2006). Range shifts and changes in phenology are the two most well-documented biological effects of changing climate conditions, but there are myriad other ways in which changes in climate have affected and will continue to affect terrestrial species and systems. Climate-induced forest mortality, for example, has been documented on all plant-covered continents (Allen *et al.*, 2010). Among other effects, climate change is altering population processes, causing biome shifts and ecosystem transitions, and changing interspecific interactions.

The magnitude and rate of climatic changes projected for the coming century will provide continued and exacerbated challenges for many terrestrial species (IPCC, 2022). Tools developed in recent years have helped scientists, managers, and planners anticipate the impacts of climate change on terrestrial species. These tools include, for example, modeling methods to forecast potential impacts, experiments that offer insights into how species or ecological communities might respond to changing climate conditions, and stepwise planning approaches to help conservation practitioners consider climate change in project design and implementation (e.g., Game *et al.*, 2011; Cross *et al.*, 2012; Wilsey *et al.*, 2013; Stein *et al.*, 2014; Swanston *et al.*, 2016).

Applying and further developing an understanding of how species and ecosystems will likely respond to future changes remains critical for developing best management practices 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 IPCC (2007) 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 species. In the past, the majority of these strategies were broad recommendations or general concepts, but increasingly, they are becoming more specific and widely accepted practices implemented on the ground.

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

Anticipating Impacts

Changes in temperature and precipitation are becoming progressively more well documented and projections from global and regional climate models continue to paint a picture of a warmer future with altered precipitation patterns (IPCC *et al.*, 2021). These changes have direct impacts on species and ecosystems. However, changes in climate also affect other earth-system processes that in turn affect biodiversity. The sections below first summarize three of these climate-driven changes that are affecting biodiversity (labeled here as climate-related drivers). The sections then go on to discuss impacts of both climate change and of these climate-related drivers on biodiversity.

Climate Related Drivers

Extreme weather events

Increases in temperature have been accompanied by changes in the frequency and severity of extreme events such as floods, heatwaves, and droughts. These extreme events are impacting species and ecosystems. As average temperatures increase and average precipitation changes, extremes will push species and ecosystems past critical thresholds in some areas (Harris *et al.*, 2018). Although many challenges exist in predicting extreme weather events (Sillmann *et al.*, 2017), there is high confidence that the frequency and intensity of extreme heat and precipitation events will continue to increase (IPCC *et al.*, 2021).

To date, much of the predictive modeling of species responses to climate change has focused on the effects of changes on long-term means, but many ecological changes will be the result of extreme climatic and weather events. A growing body of evidence documents the impacts of these heat waves, droughts, and floods on species and ecosystems. For example, a heat wave in Australia in 2011 resulted in impacts across both marine and terrestrial environments and across taxonomic groups and trophic levels (Ruthrof *et al.*, 2018). Changes in extreme weather events are resulting in heat- and drought-induced tree mortality across the U.S., particularly in the western U.S. (Clark *et al.*, 2016). Drought also has negative impacts on the flora and fauna of grasslands (Peterson *et al.*, 2021). The degree to which grasslands are resistant or resilient to drought will likely vary with local climatic conditions and current biodiversity (Huang *et al.*, 2021). In a review of 519 studies exploring the effects of extreme events on ecological systems, Maxwell *et al.* (2019) found that the majority resulted in negative impacts to plant and animal populations and that in 100 cases, populations declined by at least 25% with 31 cases of local extinction. Further, extreme events may exacerbate the impacts of other threats to species and ecosystems. For example, extreme events may aid or accelerate invasions and impacts of invasive species (Diez *et al.*, 2012).

Fire

Climate change is contributing to changes in fire regimes, which in turn have effects on populations, species, and the structures and functions of ecosystems (Kelly *et al.*, 2020). Climate change has already altered fire regimes by increasing fire severity and area burned, and these impacts are projected to continue escalating in the future (Nitschke and Innes, 2008; Littell *et al.*, 2009; Marlon *et al.*, 2009). Fire regimes and impacts are mediated by multiple factors including forest management, land use, and invasive species, in addition to climate change-related increases in CO_2 concentrations, warmer temperatures, and changes in precipitation and moisture. In the tropics for example, increases in the prevalence of fire have been linked to increased drought (Brando *et al.*, 2019). Projections of future fire risk and changes in fire regimes are produced using both empirical (e.g., de Bem *et al.*, 2018; Bjånes *et al.*, 2021) and mechanistic models (e.g., Emmett *et al.*, 2021; Keane *et al.*, 2022). These projections generally predict fire regimes that are significantly different from historical conditions (Keane *et al.*, 2008), including longer fire seasons, increased fire severity, shifts toward full crown-fires, and increases in the area burned (Malevsky-Malevich *et al.*, 2008; Nitschke and Innes, 2008; Podur and Wotton, 2010).

Increased fire severity alters community composition through the loss of non-vascular 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 such newly susceptible regions will further alter community composition (Malhi *et al.*, 2009). Climate change is also impacting fire-adapted systems. In some of these systems, decreased fire-return intervals are reducing recruitment and regeneration when fires re-occur before the new trees can produce seed. Such changes are being seen in Russian and Canadian boreal forests, temperate Australian forests, and U.S. subalpine zones (Kelly *et al.*, 2020).

Studies have also begun to explore the potential future impacts of changing fire regimes on biodiversity. Depending on the species and the nature of the change in the fire regime, some plants and animals may benefit whereas others will be negatively impacted. Studies have used mechanistic models to project impacts on biological systems including bird habitat (Regos *et al.*, 2018), plants (Bonebrake *et al.*, 2014; Emmett *et al.*, 2021), and mammals (Barber *et al.*, 2018). Recent advances in modeling include incorporating interactions between fire and other drivers of change (e.g., Bonebrake *et al.*, 2014; Keane *et al.*, 2022) and fire-vegetation feedbacks (e.g., Cochrane and Barber, 2009; Archibald *et al.*, 2018).

Sea-level rise

Climate-change-driven sea-level rise has the potential to impact both terrestrial and nearshore ecosystems. One study predicted that, of biodiverse islands around the world, those in the Caribbean, the Philippines, and Sunderland are likely to lose the most endemic species due to sea-level rise (Bellard *et al.*, 2014). Another study identified a hotspot of lichen diversity on the Atlantic Coastal Plain in the eastern U.S. to be highly vulnerable to projected increases in sea level (Lendemer and Allen, 2014). Many efforts to predict coastal impacts of sea-level rise on ecosystems have focused on transitions. For example, Rilov *et al.* (2021) predicted that sea-level rise would, in the absence of invasive rabbitfish, result in the transition of Mediterranean vermetid reefs to another diverse community, or in the presence of rabbitfish, to less diverse algal turfs. Other work has projected the potential inland shift on mangrove communities (Doyle *et al.*, 2010) or the potential transition of tidal wetlands (e.g., Thorne *et al.*, 2018a,b) found that 85% of studied tidal wetlands along the west coast of the U.S. would likely transition to unvegetated states by 2110. Horizontal migration was limited by development patterns and coastal topography. Only two of the fourteen wetlands studied were likely to be able to migrate inland.

Biodiversity Impacts

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. 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 expansions into regions of newly suitable climate and contractions away from regions of unsuitable climate can result in overall shifts in species ranges (Parmesan *et al.*, 1999; Pearson and Dawson, 2003).

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 or upward in elevation (Parmesan and Yohe, 2003; Chen *et al.*, 2011; Freeman *et al.*, 2018). 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 that are inconsistent with climatic changes (Parmesan, 2006; Chen *et al.*, 2011; Freeman *et al.*, 2018). The variation in observed range shifts likely reflects the dependence on climatic factors other than temperature (Rapacciuolo *et al.*, 2014) and non-climatic factors that also influence species distributions (Chen *et al.*, 2011; Pacifici *et al.*, 2020; Spence and Tingley, 2020). For example, precipitation change (Fei *et al.*, 2017), land-use change (Guo, Lenoir and Bonebrake, 2018), other habitat requirements (Matthews *et al.*, 2010), proximity to source populations (Melles *et al.*, 2011), species interactions (Elliott, 2011), and species traits (Pacifici *et al.*, 2020) can be important in shaping range shifts. When range shifts are driven or accelerated by climate change, they can have wide-ranging impacts on both biological and human communities by altering community composition, interspecific interactions, and ecosystem processes (Pecl *et al.*, 2017; Wallingford *et al.*, 2020). Understanding both the positive and negative impacts of range shifts is important for protecting biodiversity and sustaining ecosystem services (Wallingford *et al.*, 2020; Henry and Sorte, 2022).

The many factors that interact with climate change to influence species distributions make projecting climate impacts on species ranges challenging. Nonetheless, many studies have used predictive models to project the potential effects of climate change on species distributions. Most of these studies have used correlative species distribution models (SDMs, also referred to as bioclimatic models or niche models) that relate observed distributions of a species to current climate and use this relationship along with projections of future climate from general circulation (or "global climate") models to project future species distributions (Pearson and Dawson, 2003). Correlative SDM projections can provide useful approximations of the magnitude and location of climate-induced changes to continental biodiversity, and projections have been made for a wide array of plants and animals in most regions of the world.

Despite the widespread use of correlative SDMs, there are known uncertainties associated with the projections they produce. For example, projections are sensitive to the uncertainties associated with forecasts of future climate, the modeling techniques employed (e.g., regression-based, machine learning, Bayesian), and the predictive variables evaluated. 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; Hao *et al.*, 2019). Correlative SDMs generally do not incorporate the influence of non-climatic 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 the current relationship between a species distribution and the climate is not at equilibrium or may change under future climates (Pearson and Dawson, 2003; Dormann, 2007; Yates *et al.*, 2010). Recent studies have addressed some of these limitations by incorporating biotic interactions (Fern *et al.*, 2019; Engelhardt *et al.*, 2020), habitat factors such as vegetation (Carroll, 2010) and land-use change (Marshall *et al.*, 2018), species traits such as dispersal ability (Schloss *et al.*, 2012; Monsimet *et al.*, 2020), landscape connectivity (Monsimet *et al.*, 2020), community structure (Montesinos-Navarro *et al.*, 2018), and evolutionary abilities (Bush *et al.*, 2016) into predictive models. In addition, joint species distribution models (such as the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen *et al.*, 2017; Tikhonov *et al.*, 2020)) and generalized joint attribution models (GJAM) (Clark *et al.*, 2017) were developed to predict occurrences of multiple species simultaneously. Nonetheless, the lack of high-quality occurrence data or bias associated with the available occurrence data can compromise predictions. One recently developed approach to addressing this issue is integrating multiple data sources of occurrences (Pacifici *et al.*, 2017; Fletcher *et al.*, 2019).

Unlike correlative SDMs, which may implicitly include underlying mechanisms determining species' distributions, process-based models (also known as mechanistic SDMs) explicitly include the biophysical and/or demographic processes that drive distributions. Process-based models characterize processes and project range shifts based on relevant climate and environmental variables, species physiological tolerances, energy balance equations, morphological and behavioral traits, life history traits, and/or demographic data (Morin *et al.*, 2008; Kearney and Porter, 2009; Storkey *et al.*, 2014). Process-based models are expected to provide better predictions outside of species' current geographic and climatic ranges (Evans *et al.*, 2016; Higgins *et al.*, 2020). However, they are often data intensive and can be more challenging and costly to apply. Therefore, it is also important to be aware of the strengths and limitations of different types of process-based models when considering using them (Briscoe *et al.*, 2019).

Transitions

Climate change has already resulted in ecosystem transitions and regime shifts (Harris *et al.*, 2018), which are also projected to continue and may be widespread. Paleoecological records from the last glacial-interglacial transition indicate that we are likely to see transitions in terrestrial systems worldwide (Nolan *et al.*, 2018). Such transitions are projected to be more prevalent in Australia, New Zealand, Oceania, the Indo-Pacific region, tropical and temperate Africa, and mid-high northern latitudes (Nolan *et al.*, 2018). Recent and anticipated terrestrial transitions include shifts from forested to non-forested systems and shifts from grasslands to shrublands and woodlands. For example, changes in climate have resulted in lower recruitment in low elevation dry forests in western North America (Davis *et al.*, 2019). Conversely, woody encroachment is occurring in some tundra and savanna ecosystems (García Criado *et al.*, 2020). Changes in precipitation and increased CO_2 concentrations may be partially responsible for woody encroachment (O'Connor *et al.*, 2014).

Regime shifts are also occurring in marine systems. There are, for example, cases of oyster reefs transitioning into mangrove forests (McClenachan *et al.*, 2021) and salt marshes to mangroves (Krauss *et al.*, 2011). Australian temperate kelp forests have transitioned to seaweed turfs with faunas more representative of tropical waters (Wernberg *et al.*, 2016). Following bleaching events, some coral reefs have transitioned to macroalgae beds. One study found that coral reefs in deeper water with lower nutrient content and higher densities of herbivorous fishes and younger corals were less likely to transition and instead tended to be more resilient and more likely to bounce back after bleaching events (Graham *et al.*, 2015).

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 last 500 years across Europe (Menzel, 2005) and the appearance of spring cherry blossoms has been recorded since the 15th century in Japan (Menzel and Dose, 2005). New tools and methods have emerged and advanced for quantifying phenology, including enhanced datasets through remote sensing (e.g., Mayor *et al.*, 2017; Piao *et al.*, 2019) and crowd-sourcing (e.g., Ettinger *et al.*, 2022) and improved analytical approaches for dealing with idiosyncrasies of phenological data (Wolkovich *et al.*, 2021; e.g., Pearse *et al.*, 2017). In general, these 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, salmon migration, bird nesting, and leaf unfolding, are occurring earlier, and the vegetative growing season has lengthened (Parmesan, 2006; Feehan *et al.*, 2009; Thackeray *et al.*, 2010; Poloczanska *et al.*, 2013). In many cases, the magnitude of these changes has been greater where more warming has occurred, such as at higher elevations and latitudes (Parmesan, 2006; Feehan *et al.*, 2009; Chmura *et al.*, 2019).

Although there has been overall advancement in the timing of biological events, significant variation exists in patterns of phenological shifts across species, trophic levels, ecosystems, and geographic locations. 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 have led to concerns that asynchronies, or "phenological mismatches," may develop between interacting species, such as predators and their prey or plants and their pollinators. Although some asynchronies have been observed and may have led to reductions in fitness and population sizes (Forrest and Miller-Rushing, 2010; Miller-Rushing *et al.*, 2010; Mayor *et al.*, 2017), there is not strong evidence for widespread increases in the prevalence of phenological mismatch with climate change (Renner and Zohner, 2018; Kharouba and Wolkovich, 2020).

By combining quantified relationships between phenology and climate with future climate projections, researchers forecast how future changes in climate will affect phenology and the consequences of these potential phenological shifts (Kingsolver and Buckley, 2018; Asch, Stock and Sarmiento, 2019; MacDonald *et al.*, 2020). These forecasts often 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 phenological mismatches do not occur. For example, warming may lengthen the season of activity for multivoltine insects, leading to a greater number of generations within a year and dramatic population increases (e.g., Tobin *et al.*, 2008).

Accurate forecasting of future phenological shifts is difficult because our understanding is often based primarily on correlative observational studies. In many cases, we do not have a mechanistic understanding of controls over phenology, and the degree to which it is constrained by temperature. Even when extensive data and understanding are present, it may be problematic to project future trends from past observations. 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 concluded that warm winter conditions caused a delay in spring phases due to unmet chilling requirements. Other studies have shown that such declines in advancement could instead be due to a slow-down in spring warming (Sun *et al.*, 2021) and experimental research highlights the importance of interactions between warming with other changing conditions, such as precipitation (Ganjurjav *et al.*, 2020).

Further complicating forecasting, genetics and non-climatic cues such as photoperiod also affect phenology (Chmura *et al.*, 2019; Ettinger *et al.*, 2021). Observational and experimental data have been biased towards terrestrial plants and our knowledge of mechanisms behind observed trends in aquatic and marine systems and other organisms is limited. Even for comparatively well-studied taxa, like plants and insects, there is a need to better link phenological shifts with physiological mechanisms and fitness to both forecast and understand the implications of climate change-induced shifts (Chmura *et al.*, 2019). Mechanistic studies that determine these links, especially those that focus on mammals, amphibians, fungi, and other understudied organisms, are needed to improve our ability to anticipate future phenological changes.

Population processes

Although projected range shifts provide a coarse view of how species will likely respond to climate change, they do not capture changes occurring 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, we 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 those of 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 (Jonsson *et al.*, 2007; Estay *et al.*, 2009; Morin and Comrie, 2010; Boggs, 2016). Other populations of insects such as California montane butterflies, and other organisms, including many trees around the world and polar bears in the arctic, have experienced declines in abundance or increases in mortality associated with recent climatic changes, including temperature and drought (Molnar *et al.*, 2010; Anderegg *et al.*, 2019; Halsch *et al.*, 2021). For some species (e.g., many reptiles and some fish), offspring sex is determined by temperature, so changes in climate can alter sex ratios, which may decrease long-term population viability (Mitchell *et al.*, 2010; Geffroy and Wedekind, 2020).

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 in the U.S., the growing season has lengthened over the past 30 years, leading to declines in yellow-bellied marmot mortality, which has resulted in 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 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, our capacity to model the effects of climate change on population dynamics has improved, allowing advances such as propagating uncertainty with Bayesian modeling approaches. In recent years, studies have combined climate forecasts of species distribution models with genetically informed population viability analyses (Byer *et al.*, 2020) and spatially explicit stochastic population models (Keith *et al.*, 2008; Ooi *et al.*, 2009; Mitchell *et al.*, 2010). Such forecasts are data intensive and computationally demanding, but they facilitate a better understanding of the ecological impacts of climate change on populations.

Interspecific interactions

Climate change induced changes in geographic ranges, phenology, population dynamics, and species traits (e.g., morphological and behavioral traits) can lead to altered interspecific interactions (e.g., intensifying, weakening or decoupling current interactions, forming new interactions) and the formation of transient and novel communities (Blois *et al.*, 2013; Rafferty, 2017; Gérard *et al.*, 2020). Interacting species, such as pollinators and the plants they pollinate, may have significant differences in their physiological tolerances, life-history strategies, and dispersal abilities, and may respond to climate change differently. These differences, combined with variability in exposure to climate change, can result in mismatches (e.g., spatial, temporal, and morphological mismatches) that decouple even the strongest relationships. Also, range shifts can alter these species' recipient communities by altering original interactions and forming new interactions. Species' individualistic responses to climate change and the variety of contexts in which those responses occur (e.g., the original communities versus the recipient communities) make forecasting altered species interactions challenging. To address that challenge, scientists often combine observational or experimental studies with modeling.

Climate change affects species interactions both within and across trophic levels (e.g., symbiosis, predation, pollination, parasitism, and competition). For example, climate change may intensify pathogen infection rates (Chaloner *et al* , 2021; Mora *et al.*, 2022), weaken mutualisms involving plants and pollinators, seed dispersers, soil bacteria, and fungi (Gérard *et al.*, 2020; Keeler *et al* , 2021), enhance herbivory, particularly by insects (Descombes *et al.*, 2020; Hamann *et al.*, 2021), as well as increase predation (DeGregorio *et al.*, 2015; Bastille-Rousseau *et al.*, 2018; Peers *et al.*, 2020). Altered interspecific interactions can have cascading consequences for communities and ecosystems such as modifying nutrient cycling, simplifying food webs, lowering primary productivity, and decreasing biodiversity (Albert *et al.*, 2020; Wallingford *et al.*, 2020; Weiskopf *et al.*, 2020). These changes can have significant negative ramifications for important ecosystem services (e.g., provision of natural resources, carbon storage, natural pest control, disease regulation, and climate regulation) as well as human wellbeing (Traill *et al.*, 2010; Pecl *et al.*, 2017). Therefore, it is important to understand how different species and their interactions may respond to climate change in the future.

Although it is challenging to anticipate future effects of climate change on species interactions, scientists' ability to do so is improving with the development of various modeling approaches, advances in remote sensing technologies, and an expanded knowledge base gained from monitoring programs of both observational and experimental studies (Piao *et al.*, 2019; Hamann *et al.*, 2021). One relatively new approach is to combine data from observational or experimental studies with simulation approaches and climate forecasting. For example, for interactions affected by behavioral responses (e.g., activity patterns) to climate change, field data of predator-prey interactions between ratsnakes and bird nests were combined with spatially explicit agent-based simulation models to predict changes in interactions with future climate change (DeGregorio *et al.*, 2015). For interactions likely to be affected by distributional responses to climate change (e.g., spatial mismatch), correlative SDMs can be fit separately for interacting species to evaluate the likelihood of spatial mismatch under future climates (e.g., mismatch of a monophagous butterfly and its larval host plant, Schweiger *et al.*, 2008). Joint species distribution models can be used to predict co-occurrences of multiple species simultaneously. Process-based models that explicitly incorporate species interactions can also be used to forecast range shifts (Ponti *et al.*, 2009).

Information on species traits can also be incorporated into models to improve predictions. For example, Schleuning *et al.* (2020), proposed a trait-based framework to predict how plant-animal interactions will respond to climate change. First, traits of interacting species can be incorporated into correlative SDMs or process-based models to improve forecasts of co-occurrences. Second, matching traits (Bartomeus *et al.*, 2016), combined with projected co-occurrences, can help predict the probability of interactions and the risk of secondary extinctions in novel communities (Pichler *et al.*, 2020). Third, dispersal traits and movement models can be used to assess changes in seed dispersal. The trait-based approach requires information on species traits and their potential changes under climate change. Although the development of modeling approaches is considerably helpful, monitoring networks and observational and experimental studies are necessary to validate models and improve our understanding of species interactions and their responses to climate change.

Interactions with other stressors

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 relative to non-invasive species. 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). A meta-analysis of 361 species suggests that non-native species benefit more from climate change than native species, especially in aquatic systems (Sorte *et al.*, 2013). One possible mechanism for this asymmetry is that 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 lead to increased abundance of invasive species (Willis *et al.*, 2010). Moreover, characteristics common to invasive species such as greater dispersal abilities, faster growth rates, short generation times, and broad climatic tolerances facilitate rapid range expansion coinciding with changes in climatic conditions (Hellmann *et al.*, 2008; Schweiger *et al.*, 2010).

Bioclimatic models can forecast the extent of a species' invasive potential in a changing climate by projecting the distribution of suitable potential climate space 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 (Jarnevich and Stohlgren, 2009; Bradley *et al.*, 2010). However, not all invasive species are projected to experience climate-induced range expansions. For example, an analysis of invasive potential under climate change found that only 5 of 15 globally invasive ant species were poised to experience climate induced range expansions—the other 10 species were predicted to experience range contractions (Bertelsmeier *et al.*, 2015). Similarly, demography-based models of two invasive plant species in the northeastern U.S. produced contrasting results, with one species projected to experience a range expansion and the other a contraction. In regions where contractions are anticipated, forecasts can provide useful guidance for restoration of sites that are no longer suitable for an existing invader (Bradley and Wilcove, 2009).

Climate-change induced range shifts of native species may challenge the traditional definitions of non-native and invasive species as ranges expand beyond species' historical distributions. Previously non-invasive species have the potential to become invasive in a new region without the biological controls provided by interspecific interactions present in the previous community (Hellmann *et al.*, 2008). At the same time it should be noted that many species will be moving to track climate change and it would be counter-productive to treat all climate-tracking species as invasives to be contained, excluded, or repelled (Urban, 2020).

Land-use change

Alongside climate change, changes in land use and corresponding habitat destruction are two of the greatest threats to biodiversity (Hoffmann *et al.*, 2010; Dawson *et al.*, 2011). Studies that have explored the potential impacts of land-use changes associated with emissions scenarios and representative concentration pathways have concluded that future land-use change alone will have profound effects on biodiversity (Jantz *et al.*, 2015; Powers and Jetz, 2019). The interaction between climate change and land use may exacerbate the impacts of both stressors on flora and fauna. Recent changes in climate have likely exacerbated the effects of habitat loss and fragmentation in 18% of the world's ecosystems (Segan *et al.*, 2016).

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 potential interactions and compounding impacts of land use and climate change. For example, Higgins (2007) used a process-based dynamic global ecosystem model to forecast likely spatial shifts in climatic conditions currently associated with high species richness in northern South America. They found that the climate niche is likely to shift from an area that is less impacted by human land uses to highly modified landscapes that cannot support as many species, resulting in a reduction in overall richness. Other studies, however, have highlighted interactions between projected climate change and land-use change that are likely to result in increases in local species richness (e.g., Radinger *et al.*, 2016).

Not only will land use inhibit range expansions, but land use may also cause distributional shifts (Gehrig-Fasel *et al.*, 2007; Hockey *et al.*, 2011). 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 non-vascular 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).

Assessing how land-use change will continue to interact with climate change will require a better understanding of the mechanisms of such interactions (Schulte to Bühne *et al.*, 2021). For example, one study found a link between physiological temperature tolerance and land use: lizards in more modified landscapes had lower temperature tolerances (Lopera *et al.*, 2022). Land use may also act as an additional driver of phenological advancement, through for example, urban heat island effects that cause warmer temperatures, thus advancing 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.

Disease 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 has, and will continue to, both directly and indirectly affect the emergence and spread of parasites and disease (Canto *et al.*, 2009; Caminade *et al.*, 2019). The impacts of climate change on parasites, diseases, vectors, and hosts are individualistic and interactions between these impacts are complex (Lafferty, 2009; Thomas, 2020; Byers, 2021; Garrett *et al.*, 2021). The frequency and severity of parasite and disease outbreaks will likely increase in some environments and potentially decrease in others (Cohen *et al.*, 2020; Thomas, 2020). Changes in prevalence and severity of outbreaks have the potential to negatively impact plants and wildlife, agriculture, and human health (Patz *et al.*, 2007; Price *et al.*, 2019; Trebicki, 2020; Chaloner *et al.*, 2021).

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 (Patz *et al.*, 2008; Mas-Coma *et al.*, 2009; 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). An increase in temperature can result in increased survival of vectors and parasites (Rose *et al.*, 2016) or decreases in survival (Brown *et al.*, 2022). Although climate change may lead to the extinction of some parasites, it will lead to an increase in parasite richness in some climates (Carlson *et al.*, 2017). 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 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; Iwamura *et al.*, 2020). 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 forecast 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.*, 2008).

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 (Escobar and Craft, 2016). 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 and van Jaarsveld, 2009). Conversely, distribution modeling for the tick *Ixodes ricinus* projected much overlap in the current and projected future range, although some significant northward and eastward expansions in Europe (Alkishe *et al.*, 2017).

As for all species, non-climatic factors such as dispersal limitations, land use, and interspecific interactions may limit climate-induced range expansions (Lafferty, 2009; Cable *et al.*, 2017). However, disease and parasite distributions may be even more sensitive to non-climatic 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 diseases. 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; Callaway, 2016; Cable *et al.*, 2017). 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 non-climatic distributional determinants due to public health programs, which are often influenced by socioeconomic distributions (Rosenthal, 2009). The extensive influence of non-climatic factors on the distributions of diseases and parasites may overwhelm the impact of climate change making impacts somewhat difficult to forecast.

Human responses to climate change

People are responding to climate change in many ways. In general, these responses can be classified as either mitigation or adaptation. Mitigation actions reduce the amount that the climate will change by preventing or reducing emissions of heat-trapping gasses into the atmosphere or by sequestering carbon from the atmosphere. Such actions include, for example, efforts to improve energy efficiency and fuel economy, switching to cleaner energy power such as solar or wind, or implementing nature-based solutions —proven ways of increasing carbon sequestration and reducing greenhouse gas emissions through conservation, restoration, and improved management practices in forest, wetland, and grassland biomes (Griscom *et al.*, 2017; Seddon *et al.*, 2020).

Adaptation actions aim to prepare for or adjust to the current impacts of climate change as well as the expected impacts in the future (IPCC, 2014). Examples of conservation adaptation—efforts to help species and ecosystems adapt to the accumulating impacts of climate change—include restoring riparian areas to reduce stream temperatures, changing forest management practices to address more frequent and intense fires, and even moving populations or species to more suitable climates. Both types of responses can have positive and negative impacts on non-human species and ecosystems. Anticipating these responses and their ecological impacts will be critical for conserving biodiversity into the future (Watson, 2014).

Although both nature-based solutions and technological mitigation approaches can have both positive and negative impacts on biodiversity (Smith *et al.* 2022), nature-based solutions such as reforestation, avoided forest conversion, coastal wetland restoration, and conservation agriculture tend to generally have positive potential impacts on biodiversity (Griscom *et al.*, 2017; Fargione *et al.*, 2018). Furthermore, nature-based solutions can be designed in such a way as to have positive biodiversity outcomes (Smith *et al.*, 2022). Conversely, many technological and engineering-based solutions tend to have negative direct impacts on species and ecosystems. For example, solar and wind renewable energy installations can have impacts associated with their construction and operation with effects on physiology, behavior, and mortality rates (Agha *et al.*, 2020) as well as habitat. Effects and evidence vary by region. Thus, the design of and placement of installations and infrastructure will be critical for reducing impacts.

Many human adaptation efforts in response to climate change can be seen as a response to a change in the provision of ecosystem services. Through impacts on species, communities, and ecosystems, climate change will alter the goods and services provided by the 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 wellbeing (e.g., the provision of recreational amenities, spiritual experiences, aesthetics, 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 (Pinsky *et al.*, 2013). Climate change will also affect regulating services, which will impact the ability to grow specific crops in particular locations (Lobell and Asner, 2003; Lobell and Field, 2007; Battisti and Naylor, 2009) as well as the quantity and quality of water for drinking and irrigation (Vörösmarty *et al.*, 2000). Changes in regulating services are also affecting where people can safely live with communities displaced annually due to flooding, sea-level rise, fire, and other impacts. Although some of these displacements are the result of direct climate impacts, many are due, at least in part, to regulating services that have been compromised or surpassed. Changes in phenology, pollinator communities, soil microbial communities, the distribution of pests 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 people will adapt to climate change will be a critical step in developing adaptation strategies for species and systems. For example, climate impacts such as reduced crop production, flooding, and inundation from sea-level rise are already causing human migrations and will likely continue to do so into the future (IPCC, 2022). Such migrations will 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.

Studies have begun to project the potential effects of climate change on specific ecosystem services (e.g., Hayhoe *et al.*, 2004; Schröter *et al.*, 2005; Metzger *et al.*, 2008; Mina *et al.*, 2017; Alcamo *et al.*, 2005). Many of the methods and models that are used to assess and measure ecosystem services can be used to determine the impacts of climate change on those services (Kareiva *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 based on historical patterns or the results of surveys and other socio-economic studies.

Adaptation

Below, we discuss some of the general concepts and principles that apply to climate-change adaptation. We then provide examples of more specific adaptation strategies for protecting terrestrial species in a changing climate.

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 we manage species and systems. These concepts include assessing vulnerability, considering current and future climate in the design and implementation of projects, carefully selecting resistance, resilience, and/or transformational strategies, managing for process over composition, employing adaptive management, and, lastly, continuing to value connectivity and area protection to support adaptation.

Vulnerability

Climate change adaptation is deeply tied to the concept of vulnerability—the extent to which a species, ecosystem, or area is likely to be harmed as a result of climate change and associated stresses (Brooke, 2008). Vulnerability is generally defined as a function of three components: sensitivity, exposure, and adaptive capacity (IPCC *et al.*, 2007; Dawson *et al.*, 2011). Sensitivity refers to innate characteristics of an organism or ecosystem (e.g., tolerance to changes in temperature) that predispose a species to be 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 takes advantage of climate change. The IPCC fifth assessment report (IPCC, 2014) presented an alternative framework that uses risk, instead of vulnerability, as the overall measure of concern. Risk is defined as a function of hazard, vulnerability, and exposure. The definition of vulnerability and exposure in this framework is different from the ones mentioned previously. The framework described in the IPCC fifth assessment report has been used less often in the field of conservation (Foden *et al.*, 2019).

Accessing climate-related vulnerability (following the IPCC *et al.* (2007) definitions) or some of its three components (i.e., sensitivity, exposure, adaptive capacity) can help inform the identification, prioritization, and implementation steps of adaptation and conservation planning (Foden and Young, 2016; Prober *et al.*, 2019). Climate change vulnerability assessment is a rapidly growing field. Various vulnerability assessment approaches (e.g., attribute or trait-based, model-based, and combine approaches) have been developed and implemented (Foden *et al.*, 2019). Some vulnerability assessment approaches may not follow the framework of the three components strictly, and some focus on only one or two of the three components rather than computing an overall vulnerability score (e.g., Case *et al.*, 2015; Thurman *et al.*, 2020).

Climate change vulnerability assessments have been conducted for a wide range of targets including individual species (Foden *et al.*, 2013; Ameca *et al.*, 2019), species groups (Choe *et al.*, 2017), ecological communities (Comer *et al.*, 2012), and ecosystems (Thorne, Choe, *et al.*, 2018; Pokhriyal *et al.*, 2020). The most common outcome of a climate change vulnerability assessment is an assigned ordinal vulnerability level (e.g., low, moderate, high vulnerability) per assessment unit such as a species. There are several sources of uncertainty in vulnerability assessments including the lack of data (e.g., species trait data, occurrence data), measurement and estimation errors, and uncertainties associated with modeling processes (e.g., from projections based on climate models or species distribution models). The definition and operationalization of sensitivity and adaptive capacity can vary across assessment approaches and the difficulties in differentiating between these two vulnerability components are well recognized. Therefore, it is important to understand and validate vulnerability assessment approaches, particularly when outputs will be used to inform adaptation (Foden *et al.*, 2019).

5Ws: What, when, where, why, and who

Climate change poses risks to traditional biodiversity conservation efforts if practitioners assume that the future climate will be similar to that of the past or present. For example, more frequent and intense disturbances, such as wildfire or drought-induced tree mortality, can threaten initiatives that are designed to enhance habitat for forest-dependent species. Overlooking such climate-related risks can result in failed conservation investments and negative outcomes for people, biodiversity, and ecosystem integrity as well as lead to carbon-sink reversal. National climate commitments under the Paris Agreement likely put the world on track to warm around 2.7°C (4.5°F) above preindustrial levels by the end of the century (United Nations Environment Programme, 2021), the urgency for effective adaptation is mounting world-wide.

There is no one-size-fits-all approach to address every climate adaptation challenge. Tools for designing, managing, and evaluating adaptation efforts are becoming more prolific and increasingly critical for effective implementation. Planning approaches generally rely on a cycle of steps to define purpose and scope, assess climate impacts and vulnerabilities, review/revise goals, identify and evaluate possible actions, implement priority actions, assess effectiveness, and then iterate to incorporate emerging information. Technical guidelines and formal planning processes serve to ensure the quality of projects. However, their inherent complexity, cost, and time required can make them inaccessible or daunting, especially to small or local conservation organizations and agencies.

A tractable, rapid assessment (Box 1) enables practitioners and funders to use the "what, when, where, why, and who"—or the "5Ws"—of climate-informed action as a tool in project design and implementation (Oakes *et al.*, 2021). The "what," for example, means considering whether climate variability and projected changes will require taking new actions or modifying existing actions. The "when" asks project planners and managers to consider whether climate change influences the timing of actions, such as planting at different times of year in forest restoration. The "where" requires evaluating whether planned locations for conservation action are the best places in light of projected climate impacts. In watershed restoration, for example, a traditional conservation approach might be to restore streams that are considered prime habitat for native fish. However, warming stream temperatures could create unsuitable conditions in those streams. A climate-informed, adaptive approach would include prioritizing restoration in basins that are more likely to sustain suitable stream temperatures in the future even though more restoration might be needed to improve other aspects of habitat quality. The "why" requires managers and planners to reconsider project goals in light of projected climatic changes and the "who" asks practitioners and funders to reconsider who is involved and who benefits.

Resistance, resilience, and transformation

Conservation practices have often focused on resisting changes and maintaining historical or current conditions. However, ever-increasing impacts from climate change have highlighted the critical need to help ecosystems become more resilient or to facilitate or drive transitions towards new, more climate-adapted ecological conditions.

There are different approaches to managing systems in the face of climate change. The most commonly applied and, arguably, useful typologies have categorized conservation adaptation actions on a change continuum ranging from resistance to transformation (Peterson St-Laurent *et al.*, 2021). This continuum typically involves three categories: (1) resisting changes in order to

Box 1 Brief guide to a rapid-assessment approach using the 5Ws to help define project goals, consider climate risks, and brainstorm climate-informed actions (reproduced with permission from Oakes*et al.*, 2021).

Step 1 – Gather and examine the best-available information on current and projected climate change and its effects on nature and/or people that are the focus of the local planning effort.

Step 2 – Consider how changes in climate could impact the effectiveness of traditional actions at meeting goals and any ways in which those actions and goals may need to be modified to be more effective in a changing climate. Walk through the full suite of questions with respect to what, where, when, why to make actions climate-informed:

- WHAT (modifying tactics)– Are there ways that traditional actions need to be modified to be effective at achieving goals under a changing climate? Are there new actions that will be needed to achieve goals, or address new or exacerbated challenges caused by climate change?
- WHERE (working in strategic locations)– Are there particularly strategic places or sites to prioritize in implementation, given potential climate change impacts (e.g., work in places that are more or less likely to be impacted, or places where the chances of successful outcomes may be greatest)?
- WHEN (shifting the timing and urgency) – Do the effects of changing climate increase the urgency of actions that are already being implemented? Would such climate-informed actions need to occur at different times of the year to be effective as the climate changes?
- WHY (embracing forward-looking goals) – Even with modifications in actions, is there a need to adjust the project goals to be more realistic or feasible as the climate changes (e.g., focus on different targets, or strive for different objectives)?
- WHO (reshaping project leadership, values, and stakeholder involvement)—Who leads design and implementation, and who needs to be involved for actions to be accepted, effective, enduring, and reflective of the needs and diverse values of people and communities? Does climate change affect who benefits or should benefit from actions? Who might be harmed by actions or bear costs?

Step 3 – Document any changes to project goals and design, after taking climate change into account. If after asking the above questions you do not feel that modifications to current goals and actions are needed, document the logic of how current actions will be adequate to achieve goals even as the climate changes.

maintain current conditions (Resistance); (2) improving the capacity of a system to return to desired conditions after disturbance (Resilience); (3) allowing and/or facilitating the transition to new conditions (Transformation) (Stein *et al.*, 2013; Fisichelli *et al.*, 2016; Clifford *et al.*, 2020).

Systems that are resilient to climate change should be able to re-establish ecosystem functions and processes after a disturbance and avoid a transition to a new state as climates change. However, the meaning of the term is often still unclear in many contexts (Dudney *et al.*, 2018; Walker, 2020). Some scholars (e.g., Fisichelli *et al.*, 2016) urge practitioners to move beyond its usage, arguing that "resilience" has become increasingly vague with meanings ranging from resisting changes, to absorbing changes, and even to allowing for transformative changes through self-organization. However, it has been an attractive concept, because, if successful, it allows continued delivery of ecosystem services and, possibly, the persistence of plant and animal populations.

Other similar terminologies also exist. For example, North American researchers and agencies have proposed the Resist, Accept, or Direct (RAD) framework (Thompson *et al.*, 2021; Schuurman *et al.*, 2022). This RAD framework focuses on resource managers' actions and includes a middle category of allowing changes to occur without interference. By contrast, Resistance, Resilience, Transformation (R-R-T) focuses more on a combination of actions and primary objectives, in an effort to respond to, and cope with, changes occurring as a result of climate change.

Peterson St. Laurent *et al.* (2021) developed a 6-point scale to better distinguish between these concepts (**Fig. 1**). Ranging from active resistance to accelerated transformation, the R-R-T continuum represents progressively greater acceptance of changes in ecosystem structure and function. Examples on one end of the continuum include eradicating non-native species in specific ecosystems as "Active Resistance." On the other end, using assisted migration to move species outside of their current or historical range falls into the category of "Accelerated Transformation" (**Table 1**).

When applying the R-R-T scale to a case study of 104 adaptation projects in the United States funded between 2011 and 2019, researchers found a trend that involved an increasing use of transformational practices, which varied across ecosystems. Though approaches like species translocation have been controversial in conservation history (Hagerman *et al.*, 2010; Hagerman *et al.*, 2010), practitioners are more commonly turning to such novel actions in response to the direct and indirect impacts—as well as potential impacts—of changing climatic conditions (**Fig. 2**).

Managing for process over composition

Because changes in climate are driving shifts in phenology, populations, and distributions, managing for particular assemblages of species may not be reasonable. Such shifts may also result in systems that are more resilient to climate change. Many have suggested that these climate-change-induced shifts necessitate a move from managing for particular species and communities to managing for ecosystem processes, often with shifting baselines (Harris *et al.*, 2006; Heller and Zavaleta, 2009; Hobbs *et al.*, 2009). Others have proposed that climate-smart management should use a rates-focused framework to consider rates of change for ecological processes, including strategies to both slow and accelerate these rates in order to reduce mismatch among climate and ecological rates of change (Williams *et al.*, 2021). Managing for ecosystem function or ecological rate of change requires a forward-looking approach, sometimes incorporating new species introductions.

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 for managing uncertain systems, making it potentially a highly useful approach to dealing with climate change (Arvai *et al.*, 2006). To address climate change, adaptive management approaches tend to have four basic steps that can be iteratively repeated (Kareiva *et al.*, 2008). The first step involves 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, are designed to address one 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. A challenge of implementing adaptive management approaches for tackling climate change is that the time required to complete activities from planning to implementation and monitoring might be outpaced by rates of climate change and associated ecological responses on the ground (Morelli *et al.*, 2016; Balantic *et al.*, 2021).

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 one of the most commonly recommended adaptation approaches for addressing climate impacts on biodiversity (Heller and Zavaleta, 2009; McLaughlin *et al.*, 2022).

In the past, suggested strategies for improving connectivity to address climate change have been somewhat general—e.g., placing new reserves between existing reserves, creating a system of stepping-stone reserves, or adding reserves in close proximity to existing reserves (Lawler, 2009; Mawdsley *et al.*, 2009). Researchers have recently developed more sophisticated approaches to connecting landscapes to address climate change, which can be grouped into four categories (Littlefield *et al.*, 2019). One set of approaches uses projected climatic trajectories or climate analogs to define corridors and movement routes; for example, mapping

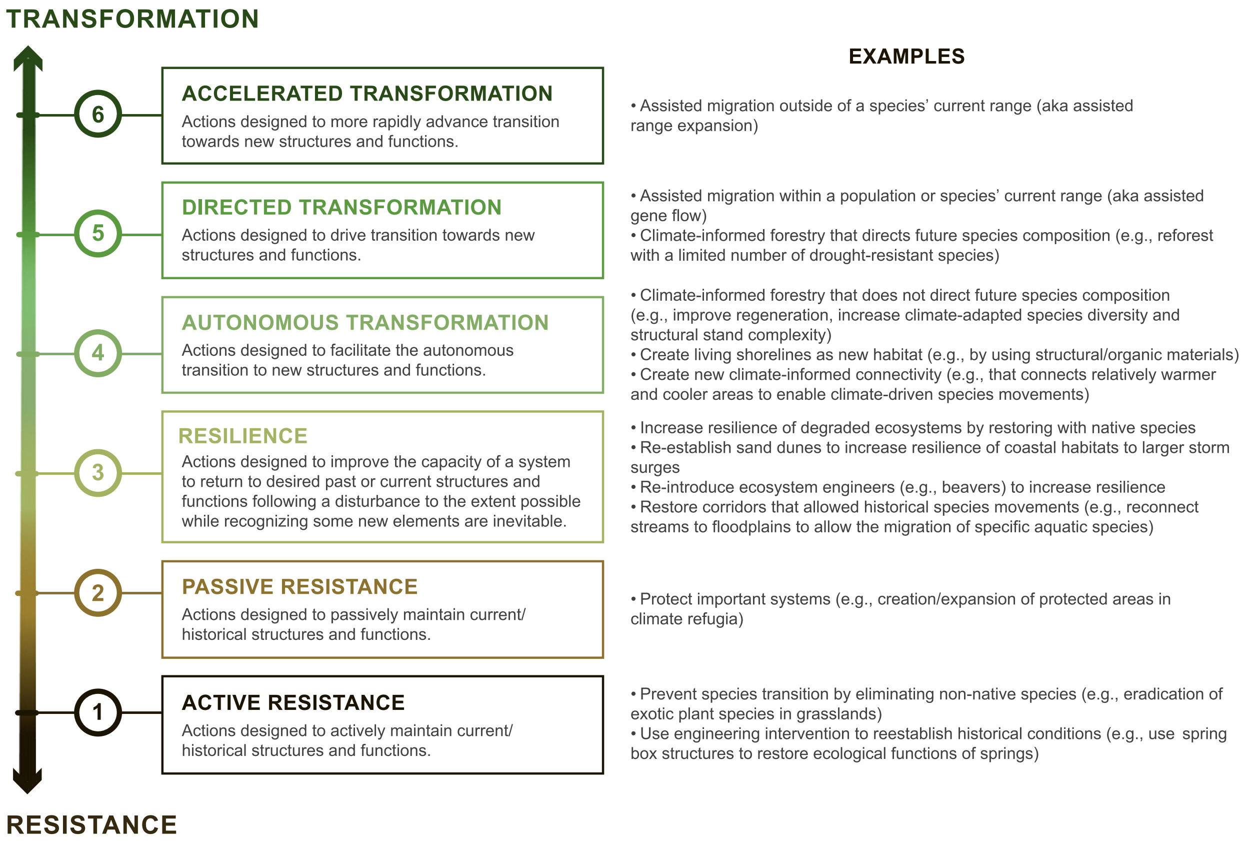

Fig. 1 Resistance-Resilience-Transformation (R-R-T) Scale with definitions. The R-R-T scale is a six-point continuous interval scale representing a continuum spanning from actively resisting changes to accelerating transformation towards new, more climate-adapted conditions. Reprinted from Peterson St-Laurent, G., Oakes, L.E., Cross, M. and Hagerman, S. (2021). R-R-T (resistance–resilience–transformation) typology reveals differential conservation approaches across ecosystems and time. Communications Biology 4 (1), 1–9. https://doi.org/10.1038/s42003-020-01556-2.

potential movement corridors that connect current climate conditions to their future analogs (Littlefield *et al.*, 2019). A second set of approaches uses projected shifts in species distributions to identify potential routes for species to move from current to future suitable (Williams *et al.*, 2005; Lawler *et al.*, 2013; Alagador *et al.*, 2014). A third group of approaches maps corridors based on current climatic gradients; these include mapping routes that go from warmer to cooler areas (Nuñez *et al.*, 2013; McGuire *et al.*, 2016), follow riparian corridors (Krosby *et al.*, 2018), or track elevational or latitudinal gradients (Anderson *et al.*, 2016). Finally, a fourth set of approaches attempts to connect combinations of geophysical features, such as land facets or geophysical settings to define corridors (Brost and Beier, 2012).

Although it is important to identify potential movement corridors, increasing the permeability of the landscape is also critical (Franklin and Lindenmayer, 2009). It may be possible to manage lands to facilitate species' movements in response to climate change through transformational adaptation strategies. For example, selective harvest or retention cuts, tree-planting, and rotational grazing may provide habitat to facilitate range expansions (Kohm and Franklin, 1997; Manning *et al.*, 2009). It is possible to prioritize areas for these incentives and management actions using similar approaches that are used for reserve selection and the siting of protected areas.

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 currently 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 while 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

Table 1 Examples of adaptation actions and their primary objective for the six categories of the "R-R-T scale"

Categories	*Examples of actions*	*Primary objective*
1. Active Resistance	Eradicate non-native species in grassland or forest ecosystems.	Actively prevent changes in species composition.
	Install and manage water control structures to maintain historical water levels in a coastal impoundment.	Actively resist rising sea levels.
2. Passive Resistance	Create or expand protected areas in climate refugia.	Passively maintain current ecosystems.
	Purchase conservation easements to protect a species that is endangered by climate change.	Passively protect species in their historical habitat.
3. Resilience	Reconnect previously existing corridors to allow the migration of specific species.	Enhance the ability of species to persist as climate changes by removing barriers to movement and dispersal
	Restore streams by reintroducing beaver.	Increase resilience of stream functions to natural disturbances such as floods and droughts.
4. Autonomous Transformation	Connect relatively warmer and colder aquatic areas.	Create opportunities for species movements to seek cold water refugia.
	Apply forestry techniques designed to increase native species diversity.	Increase chances that some species will thrive as climate changes.
5. Directed Transformation	Use assisted migration by planting with seeds gathered in a warmer part of a species' current range (aka assisted gene flow).	Drive transition towards climate-adapted genetic composition of species or populations.
	Use climate-informed forestry to direct future species composition (e.g., post-harvest planting using drought-resistant native species).	Drive transition towards more climate-adapted native species compositions.
6. Accelerated Transformation	Use assisted migration to move a species outside of its current or historical range (aka assisted range expansion).	Accelerate climate-driven species transition.
	Restore riparian ecosystems by inoculating soils with non-native inoculant materials that are adapted to warmer and drier conditions.	Accelerate transition towards more climate-adapted ecosystem functions.

Note: Adpoted from Peterson St-Laurent, G., Oakes, L.E., Cross, M. and Hagerman, S. (2021). R-R-T (resistance–resilience–transformation) typology reveals differential conservation approaches across ecosystems and time. Communications Biology 4 (1), 1–9. doi:10.1038/s42003-020-01556-2.

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 elevations 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; Stralberg *et al.*, 2018). 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 likely 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 locating 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 (Lawler *et al.*, 2015). 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). Others have stressed geologic variability in a reserve network (Anderson and Ferree, 2010; Anderson *et al.*, 2014), 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).

Other abiotic-based strategies aim to protect areas projected to serve as climate refugia. Researchers have defined climate refugia in multiple ways (Ashcroft, 2010; Morelli *et al.*, 2016). Most, however, defined climate refugia either as places where the climate will change less than in the surrounding landscape and thus species may be able to remain as the climate changes or places that will have suitable climates for species in the future and thus places to which species might move as the climate changes. Refugia

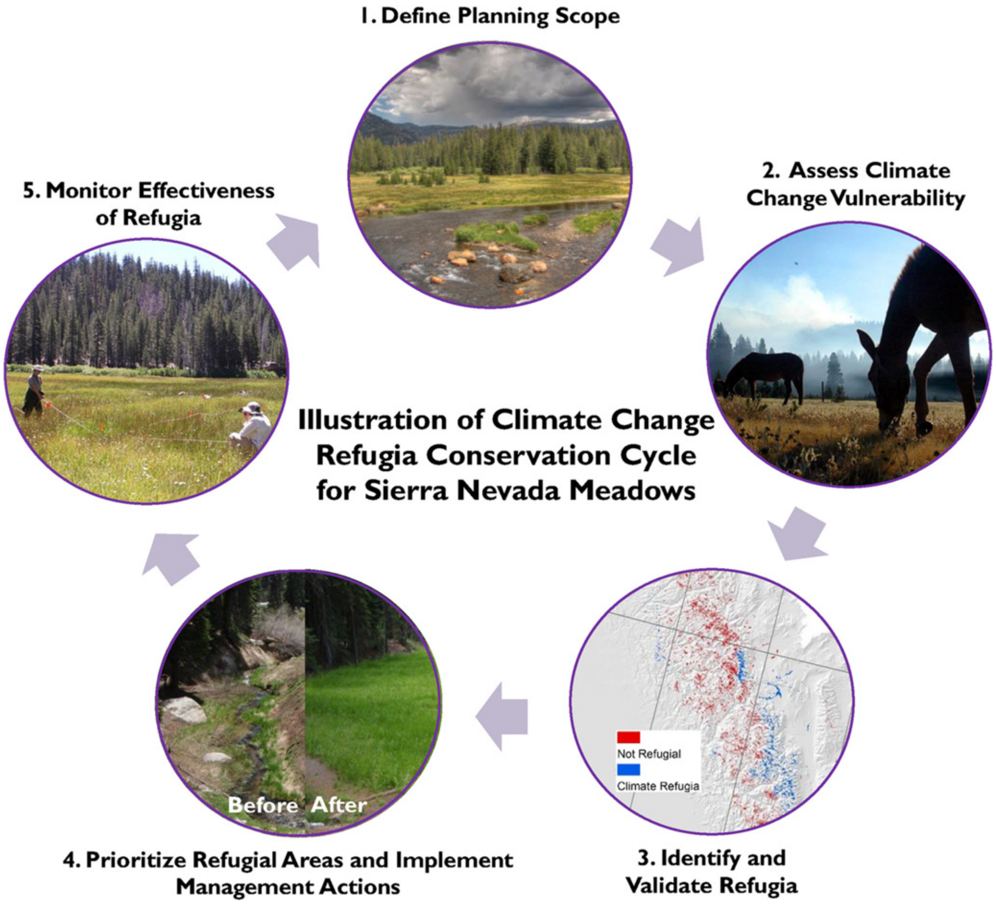

Fig. 2 Adaptive management cycle for climate refugia conservation. Balantic, C., Adams, A., Gross, S. *et al.* (2021). Toward climate change refugia conservation at an ecoregion scale. Conservation Science and Practice 3 (9), e497. https://doi.org/10.1111/csp2.497.

have also been defined at different spatial scales. Macrorefugia occur at larger extents and have been mapped using multiple approaches. One such approach involves using projected shifts in species distributions to identify where species might remain as the climate changes (Stralberg *et al.*, 2018). Others have identified where the climate is projected to change less (Game *et al.*, 2011; Belote *et al.*, 2018), the future location of analogs of current climates that are projected to become increasingly rare (Michalak *et al.*, 2018), and where environmental diversity is high or where climate velocities are low (Carroll *et al.*, 2017).

Another suggested approach to designing networks of protected areas that will conserve species in a changing climate involves the use of dynamic reserves. By allowing the boundaries of protected areas to move through time, a selected set of areas might be able to accommodate species movements. Strange *et al.* (2011) demonstrated a dynamic reserve-selection approach to address climate-driven changes in habitat suitability. Since then, a relatively small number of studies have taken a dynamic reserve selection approach to account for shifting species distributions (Alagador *et al.*, 2014). Others have suggested integrated networks of permanent and transitory protected areas (D'Aloia *et al.*, 2019).

Given the uncertainties associated with species responses to climate change, no one single approach is likely to be sufficient to address climate-driven shifts in species distributions. Not surprisingly, a number of studies have begun to incorporate several of the concepts described in this section into the conservation planning process. Carroll *et al.* (2010) included projected future species distributions and potential refugia. Game *et al.* (2011) included climate refugia, connectivity, and geophysical settings into their prioritized reserve network. Similarly, Lawler *et al.* (2020) incorporated projected species distributions, climate corridors, and climate refugia into selected reserve networks.

Adaptation Actions and Joint Adaptation and Mitigation

Policies and negotiations have often treated adaptation and mitigation separately because they pursue different objectives and operate at different spatial and temporal scales; mitigation provides benefits for global climate in the long term, whereas adaption tends to provide more local benefits that accrue in the short term as well as longer term (Swart and Raes, 2007). Adaptation is a concern that local policymakers and citizens can address from the bottom-up, whereas mitigation is often regarded as a challenge that requires top-down regulation at the international level (Kongsager, 2018). In practice, actions that contribute to both objectives can increase the efficiency of financial allocations and minimize trade-offs, particularly in land-related activities such as forest management and conservation (Locatelli *et al.*, 2015). Synergies between the two, as defined in the fourth IPCC Assessment Report IPCC *et al.* (2007), can be understood as the "interaction of adaptation and mitigation so that their combined effect is greater than the sum of their effects if implemented separately." Projects can have "joint outcomes," relating to activities with non-climatic primary objectives that deliver both adaptation and mitigation outcomes; unintended side effects, because focusing on one climate objective—adaptation or mitigation—can deliver outcomes for the other; and joint objectives when both adaptation and mitigation objectives were considered from the start (Locatelli *et al.*, 2015).

Agriculture, forestry, and urban development offer many opportunities for synergies in adaptation and mitigation. Many agricultural actions, for example, involve the use of land and water resources and thus, projects designed to benefit species and ecosystems in these working landscapes have potential to deliver both adaptation and mitigation benefits. Innovative actions could result in sequestering carbon in soils, while strengthening an ecosystem's resilience to current and future climate impacts. In forest ecosystems, changing management intensity and species composition, or altering fire regimes could result in multiple benefits. Actions that support mitigation in urban areas are typically related to energy and water use efficiency, as well as increasing green areas (Nordic Council of Ministers, 2017).

In terms of tradeoffs, it is also important to note that it is unlikely that planners will be able to *optimize* for multiple objectives in any one initiative without a compromise of one or both outcomes to some degree. Not surprisingly, studies have demonstrated that explicitly targeting multiple objectives will result in trade-offs. For example, in a study conducted on a restoration effort in a highly modified catchment in New Zealand, researchers found significant trade-offs between biodiversity gains and reduction of environmental impacts, such as nitrogen leaching, greenhouse gas emissions, and erosion (Mason *et al.*, 2012). Conservation planning analyses across the Americas and Britain reveal that a carbon-only strategy would not be effective at conserving biodiversity; a combined carbon-biodiversity strategy could protect 90% of carbon stocks (relative to a carbon-only strategy) and 90% of the biodiversity (relative to a biodiversity- only strategy) in both regions (Thomas *et al.*, 2013). This suggests a need to integrate multiple objectives from the onset of project design to reach efficient compromises; the authors conclude that "combining carbon and species within a single conservation planning framework, large increases in biodiversity gains could be achieved for only a small reduction in the amount of carbon stocks maintained within a single protected ecosystem." These considerations for biodiversity are likely most applicable to planting initiatives and restoration of degraded forests that aim, primarily, to enhance carbon sequestration, as opposed to protection of healthy intact forests that harbor high carbon stocks, high diversity of forest-dependent species, and high functional diversity (Watson *et al.*, 2018).

Drawing from a portfolio of projects funded by the Wildlife Conservation Society Climate Adaptation Fund, we provide examples of adaptation and joint mitigation-adaptation initiatives implemented across U.S. states, commonwealths, territories, and tribal lands. The Climate Adaptation Fund, supported by a grant to Wildlife Conservation Society from the Doris Duke Charitable Foundation, provided $24 million in funding for 123 adaptation projects between 2011 and 2021; a subset of projects was considered to jointly address adaptation and mitigation. These examples offer further insight into climate-informed conservation strategies, offering adaptation or adaptation and mitigation benefits, that have been implemented in recent years.

In the Southern Appalachian Mountains of western North Carolina, warming temperatures have caused a reduction in habitat for cool water aquatic species, and changes in precipitation patterns have also affected base flow, flood severity, and frequency of floods. This "resistance" project, led by Trout Unlimited, addressed two major threats to aquatic populations in the biologically diverse Southern Appalachians: (1) small population size (or 'patch size') due to stream fragmentation, and (2) inability of fish and other aquatic fauna to move to find cold water, spawning habitat, and suitable juvenile and adult habitat. Actions included targeting watersheds shown to have a low sensitivity to warming and a high potential for reconnecting cold water habitats through conservation and restoration.

Forests provide critical habitat, protect freshwater sources, and store carbon. In Colorado, many forests are impacted by climate change and wildfires that leave the land scorched. Unable to recover, vast areas may convert to shrub- or grasslands. The Nature Conservancy aimed to increase forest resilience in ponderosa pine forests in this joint mitigation-adaptation project. Focusing on "resilience" actions and outcomes, the project team worked to reforest severely burned areas and apply thinning and prescribed burning to protect seed trees and habitat.

The Lower Rio Grande Valley, a fertile delta for the Rio Grande River in South Texas, is home to a native Texas thornscrub forest that serves as a habitat for more than a hundred songbird species and butterfly species, as well as eleven threatened and endangered species, including the ocelot. Land-use decisions dramatically reduced the forested area, leaving much of it fragmented. Climate models predict that this area will be further affected by drought due to increased temperatures and decreased rainfall. Led by American Forests, this project aimed to restore 270 acres of degraded ranch lands to functioning thornscrub forest and promote drought resilience by planting drought-tolerant species, using tree shelters to retain soil moisture, and planting in locations that could serve as migration corridors for wildlife into the future. Two hundred and seventy thousand seedlings were planted. The estimates at the start of the project indicated about 100,000 tons of carbon could be stored over 50 years. This project included "directed transformation" strategies: shifting species composition to a community more likely to survive future conditions.

In the northwestern Hawaiian Islands, sea-level rise and increasing storm surges associated with climate change have threatened black-footed albatrosses, Bonin petrels, and Tristram's storm petrels, which nest in low-lying atolls. An "accelerated transformation" project led by Pacific Rim Conservation aimed to restore habitat through transplanting native species and invasive plant removal and protect populations by translocating seabirds to coastal dune habitat that can withstand projected sea-level rise.

As a final example, several projects funded by the Climate Adaptation Fund have used beaver reintroductions and the installation of beaver-dam analogs to restore functioning floodplains, improve riparian and instream habitat, create cold water refugia, and increase water storage capacity. All of these outcomes can make streams and riparian ecosystems more resilient to drought and heavy precipitation events that are occurring with increasing frequency with climate change. Beaver dam analogs are human created structures that mimic beaver dams, slowing flow and increasing stream sinuosity. These structures can also change riparian vegetation and help attract beaver to a site. Conservation objectives of these projects have often included increasing cold water fish populations, restoring riparian plant communities, and rebuilding functioning floodplains.

Many of these actions also fall into what Prober *et al.* (2019) term to be "ecological renovation"—management and nature conservation actions that actively allow for environmental change. "Renovate," as the authors discuss, means to repair or improve upon something, to remodel or impart new vigor and revive. "Restoration", by contrast, is often defined as bringing back to an original or normal condition, which may not be possible. They propose a typology of 23 intervention options to facilitate persistence or adaptation of biodiversity and ecosystems in a changing climate. Examples include assisting species to reach and establish within projected suitable environments outside their current range, promoting adaptation by promoting genetic diversity, and facilitating species' persistence by targeting climate-resilient locations.

Co-benefits of adaptation strategies

Here, we define the co-benefits of adaptation as the positive effects that an adaptation strategy designed to address a specific human need has on non-human species, communities, or ecosystems, or conversely the positive effects on human well-being of adaptation strategies designed to help non-human 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; Fargione *et al.*, 2018). Similar co-benefits of adaptation strategies have not been as well documented, but these co-benefits will likely arise in many instances.

Some adaptation strategies that target human wellbeing will have biodiversity benefits. For example, planting trees and shrubs in urban areas to reduce heat-island effects could provide habitat for some animals. Similarly, planting of bioswales and rain gardens to reduce runoff and flooding could provide habitat for other species. Moving homes out of floodplains and away from shorelines could benefit riparian, aquatic, and intertidal species.

There are also clear co-benefits for human health and well-being that are likely to result from adaptation strategies that restore coastal habitats, riparian areas, and floodplains. Removing seawalls, 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 -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 non-human 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 non-human 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 requires an understanding of how climate change will affect species and ecosystems. Much is already known about climate effects on phenologies, distributions, populations, interspecific interactions, and diseases and pathogens. Although there remain significant gaps in our knowledge of these effects, detailed studies of potential climate impacts on only specific species are not likely to provide managers and policy makers with the most critical information for developing adaptation strategies for ecosystems and ecological communities. Actionable adaptation strategies that have already been developed and continue to be improved with ongoing research and "learning by doing" have the potential to inform the management of a wide range of ecosystems and the species within them. Further research on, and sharing of, approaches to adaptive management, connecting landscapes to facilitate range shifts, and measuring and valuing the co-benefits of adaptation strategies for human and natural systems will be critical to address future climate impacts on terrestrial species and ecosystems.

References

Agha, M., Lovich, J. E., Ennen, J. R. and Todd, B. D. (2020) Wind, sun, and wildlife: Do wind and solar energy development `short-circuit' conservation in the western United States? Environmental Research Letters 15 (7), 075004. https://doi.org/10.1088/1748-9326/ab8846.

Alagador, D., Cerdeira, J. O. and Araújo, M. B. (2014) Shifting protected areas: Scheduling spatial priorities under climate change. Journal of Applied Ecology 51 (3), 703–713. https://doi.org/10.1111/1365-2664.12230.

Albert, S., Flores, O. and Strasberg, D. (2020) Collapse of dispersal trait diversity across a long-term chronosequence reveals a strong negative impact of frugivore extinctions on forest resilience. Journal of Ecology 108 (4), 1386–1397. https://doi.org/10.1111/1365-2745.13359.

Alkishe, A. A., Peterson, A. T. and Samy, A. M. (2017) Climate change influences on the potential geographic distribution of the disease vector tick Ixodes ricinus. PLOS ONE 12 (12), e0189092. https://doi.org/10.1371/journal.pone.0189092.

Allen, C. D., Macalady, A. K. and Chenchouni, H. *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259 (4), 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Ameca, E. I., Mace, G. M., Cowlishaw, G. and Pettorelli, N. (2019) Relative vulnerability to hurricane disturbance for endangered mammals in Mexico: A call for adaptation strategies under uncertainty. Animal Conservation 22 (3), 262–273. https://doi.org/10.1111/acv.12461.

Anderegg, W. R., Anderegg, L. D., Kerr, K. L. and Trugman, A. T. (2019) Widespread drought-induced tree mortality at dry range edges indicates that climate stress exceeds species' compensating mechanisms. Global change biology 25 (11), 3793–3802.

Anderson, M. G. and Ferree, C. E. (2010) Conserving the stage: Climate change and the geophysical underpinnings of species diversity. PLOS ONE 5 (7), e11554.

Anderson, M. G., Clark, M. and Sheldon, A. O. (2014) Estimating climate resilience for conservation across geophysical settings. Conservation Biology 28 (4), 959–970. https://doi.org/10.1111/cobi.12272.

Alcamo, J., Vuuren, D. v. and Ringler, C., *et al.* (2005). Changes in nature's balance sheet: model-based estimates of future worldwide ecosystem services. Ecology and Society. 10(2), Art. 19.

Anderson, M.G., Barnett, A. and Clark, M. *et al.* (2016). Resilient and connected landscapes for terrestrial conservation. The Nature Conservancy, Eastern Conservation Science, Eastern Regional Office Boston, MA. pp. 1–149.

Araújo, M. B., Cabeza, M., Thuiller, W., Hannah, L. and Williams, P. H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10 (9), 1618–1626.

Archibald, S., Lehmann, C. E. R. and Belcher, C. M. *et al.* (2018) Biological and geophysical feedbacks with fire in the Earth system. Environmental Research Letters 13 (3), 033003. https://doi.org/10.1088/1748-9326/aa9ead.

Arvai, J., Bridge, G. and Dolsak, N. *et al.* (2006) Adaptive management of the global climate problem: Bridging the gap between climate research and climate policy. Climatic Change 78 (1), 217–225.

Asch, R. G., Stock, C. A. and Sarmiento, J. L. (2019) Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Global Change Biology 25 (8), 2544–2559.

Ashcroft, M. B. (2010) Identifying refugia from climate change. Journal of Biogeography 37 (8), 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x.

Balantic, C., Adams, A. and Gross, S. *et al.* (2021) Toward climate change refugia conservation at an ecoregion scale. Conservation Science and Practice 3 (9), e497. https://doi.org/10.1111/csp2.497.

Barber, Q. E., Parisien, M.-A. and Whitman, E. *et al.* (2018) Potential impacts of climate change on the habitat of boreal woodland caribou. Ecosphere 9 (10), e02472. https://doi.org/10.1002/ecs2.2472.

Bartomeus, I., Gravel, D. and Tylianakis, J. M. *et al.* (2016) A common framework for identifying linkage rules across different types of interactions. Functional Ecology 30 (12), 1894–1903. https://doi.org/10.1111/1365-2435.12666.

Bastille-Rousseau, G., Schaefer, J. A. and Peers, M. J. L. *et al.* (2018) Climate change can alter predator–prey dynamics and population viability of prey. Oecologia 186 (1), 141–150. https://doi.org/10.1007/s00442-017-4017-y.

Battisti, D. S. and Naylor, R. L. (2009) Historical warnings of future food insecurity with unprecedented seasonal heat. Science 323 (5911), 240–244.

Beier, P. and Brost, B. (2010) Use of land facets to plan for climate change: Conserving the arenas, not the actors. Conservation Biology 24 (3), 701–710.

Bellard, C., Leclerc, C. and Courchamp, F. (2014) Impact of sea level rise on the 10 insular biodiversity hotspots. Global Ecology and Biogeography 23 (2), 203–212. https://doi.org/10.1111/geb.12093.

Belote, R. T., Carroll, C. and Martinuzzi, S. *et al.* (2018) Assessing agreement among alternative climate change projections to inform conservation recommendations in the contiguous United States. Scientific Reports 8 (1), 9441. https://doi.org/10.1038/s41598-018-27721-6.

de Bem, P. P., Júnior, O. A. and de, C. *et al.* (2018) Predicting wildfire vulnerability using logistic regression and artificial neural networks: A case study in Brazil's Federal District. International Journal of Wildland Fire 28 (1), 35–45. https://doi.org/10.1071/WF18018.

Bernhardt, E. L., Hollingsworth, T. N. and Chapin, F. S. (2011) Fire severity mediates climate-driven shifts in understorey community composition of black spruce stands of interior Alaska. Journal of Vegetation Science 22 (1), 32–44.

Bertelsmeier, C., Luque, G. M., Hoffmann, B. D. and Courchamp, F. (2015) Worldwide ant invasions under climate change. Biodiversity and Conservation 24 (1), 117–128. https://doi.org/10.1007/s10531-014-0794-3.

Bjånes, A., De La Fuente, R. and Mena, P. (2021) A deep learning ensemble model for wildfire susceptibility mapping. Ecological Informatics 65, 101397. https://doi.org/10.1016/j.ecoinf.2021.101397.

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C. and Finnegan, S. (2013) Climate change and the past, present, and future of biotic interactions. Science 341 (6145), 499–504. https://doi.org/10.1126/science.1237184.

Boggs, C. L. (2016) The fingerprints of global climate change on insect populations. Current Opinion in Insect Science 17, 69–73.

Bonebrake, T. C., Syphard, A. D. and Franklin, J. *et al.* (2014) Fire management, managed relocation, and land conservation options for long-lived obligate seeding plants under global changes in climate, urbanization, and fire regime. Conservation Biology 28 (4), 1057–1067. https://doi.org/10.1111/cobi.12253.

Bradley, B. A. and Wilcove, D. S. (2009) When invasive plants disappear: Transformative restoration possibilities in the Western United States resulting from climate change. Restoration Ecology 17 (5), 715–721.

Bradley, B. A., Wilcove, D. S. and Oppenheimer, M. (2010) Climate change increases risk of plant invasion in the Eastern United States. Biological Invasions 12 (6), 1855–1872.

Brando, P. M., Paolucci, L. and Ummenhofer, C. C. *et al.* (2019) Droughts, wildfires, and forest carbon cycling: A pantropical synthesis. Annual Review of Earth and Planetary Sciences 47 (1), 555–581. https://doi.org/10.1146/annurev-earth-082517-010235.

Briscoe, N. J., Elith, J. and Salguero-Gómez, R. *et al.* (2019) Forecasting species range dynamics with process-explicit models: Matching methods to applications. Ecology Letters 22 (11), 1940–1956. https://doi.org/10.1111/ele.13348.

Brooke, C. (2008) Conservation and adaptation to climate change. Conservation Biology 22 (6), 1471–1476.

Brooks, D. R. and Hoberg, E. P. (2007) How will global climate change affect parasite-host assemblages? Trends in Parasitology 23 (12), 571–574.

Brost, B. and Beier, P. (2012) Use of land facets to design linkages for climate change. Ecological Applications 22, 87–103.

Brown, C. R., Hannebaum, S. L., Eaton-Clark, A., Booth, W. and O'Brien, V. A. (2022) Elevated temperature reduces overwintering survival of an avian ectoparasite, the swallow bug (Hemiptera: Cimicidae: Cimex vicarius). Environmental Entomology 51 (2), 513–520. https://doi.org/10.1093/ee/nvac015.

Buisson, L., Thuiller, W., Casajus, N., Lek, S. and Grenouillet, G. (2010) Uncertainty in ensemble forecasting of species distribution. Global Change Biology 16 (4), 1145–1157. https://doi.org/10.1111/j.1365/2486.2009.02000.x.

Bush, A., Mokany, K. and Catullo, R. *et al.* (2016) Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecology Letters 19 (12), 1468–1478. https://doi.org/10.1111/ele.12696.

Byer, N. W., Reid, B. N. and Peery, M. (2020) Genetically-informed population models improve climate change vulnerability assessments. Landscape ecology 35 (5), 1215–1228.

Byers, J. E. (2021) Marine parasites and disease in the era of global climate change. Annual Review of Marine Science 13 (1), 397–420. https://doi.org/10.1146/annurev-marine-031920-100429.

Cable, J., Barber, I. and Boag, B. *et al.* (2017) Global change, parasite transmission and disease control: Lessons from ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 372 (1719), 20160088. https://doi.org/10.1098/rstb.2016.0088.

Caffarra, A. and Eccel, E. (2011) Projecting the impacts of climate change on the phenology of grapevine in a mountain area. Australian Journal of Grape and Wine Research 17 (1), 52–61.

Callaway, E. (2016) Dogs thwart effort to eradicate Guinea worm. Nature 529 (7584), 10–11. https://doi.org/10.1038/529010a.

Caminade, C., McIntyre, K. M. and Jones, A. E. (2019) Impact of recent and future climate change on vector-borne diseases. Annals of the New York Academy of Sciences 1436 (1), 157–173. https://doi.org/10.1111/nyas.13950.

Canto, T., Aranda, M. A. and Fereres, A. (2009) Climate change effects on physiology and population processes of hosts and vectors that influence the spread of hemipteran-borne plant viruses. Global Change Biology 15 (8), 1884–1894.

Carlson, C. J., Burgio, K. R. and Dougherty, E. R. *et al.* (2017) Parasite biodiversity faces extinction and redistribution in a changing climate. Science Advances 3 (9), e1602422. https://doi.org/10.1126/sciadv.1602422.

Carroll, C. (2010) Role of climatic niche models in focal-species-based conservation planning: Assessing potential effects of climate change on Northern Spotted Owl in the Pacific Northwest, USA. Biological Conservation 143 (6), 1432–1437. https://doi.org/10.1016/j.biocon.2010.03.018.

Carroll, C., Roberts, D. R. and Michalak, J. L. *et al.* (2017) Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. Global Change Biology 23 (11), 4508–4520. https://doi.org/10.1111/gcb.13679.

Case, M. J., Lawler, J. J. and Tomasevic, J. A. (2015) Relative sensitivity to climate change of species in northwestern North America. Biological Conservation 187, 127–133. https://doi.org/10.1016/j.biocon.2015.04.013.

Chaloner, T. M., Gurr, S. J. and Bebber, D. P. (2021) Plant pathogen infection risk tracks global crop yields under climate change. Nature Climate Change 11 (8), 710–715. https://doi.org/10.1038/s41558-021-01104-8.

Chen, I. C., Hill, J. K., Ohlemueller, R., Roy, D. B. and Thomas, C. D. (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333 (6045), 1024–1026.

Chmura, H. E., Kharouba, H. M. and Ashander, J. *et al.* (2019) The mechanisms of phenology: The patterns and processes of phenological shifts. Ecological Monographs 89 (1), e01337.

Choe, H., Thorne, J. H. and Hijmans, R. *et al.* (2017) Meta-corridor solutions for climate-vulnerable plant species groups in South Korea. Journal of Applied Ecology 54 (6), 1742–1754. https://doi.org/10.1111/1365-2664.12865.

Clark, J. S., Iverson, L. and Woodall, C. W. *et al.* (2016) The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology 22 (7), 2329–2352. https://doi.org/10.1111/gcb.13160.

Clark, J. S., Nemergut, D., Seyednasrollah, B., Turner, P. J. and Zhang, S. (2017) Generalized joint attribute modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. Ecological Monographs 87 (1), 34–56. https://doi.org/10.1002/ecm.1241.

Clifford, K. R., Yung, L. and Travis, W. R. *et al.* (2020) Navigating climate adaptation on public lands: How views on ecosystem change and scale interact with management approaches. Environmental Management 66 (4), 614–628. https://doi.org/10.1007/s00267-020-01336-y.

Cochrane, M. A. and Barber, C. P. (2009) Climate change, human land use and future fires in the Amazon. Global Change Biology 15 (3), 601–612. https://doi.org/10.1111/j.1365-2486.2008.01786.x.

Cohen, J. M., Sauer, E. L., Santiago, O., Spencer, S. and Rohr, J. R. (2020) Divergent impacts of warming weather on wildlife disease risk across climates. Science 370 (6519), 1702. https://doi.org/10.1126/science.abb1702. (eabb).

Colombaroli, D., Marchetto, A. and Tinner, W. (2007) Long-term interactions between Mediterranean climate, vegetation and fire regime at Lago di Massaciuccoli (Tuscany, Italy). Journal of Ecology 95 (4), 755–770.

Comer, P., Young, B., Schulz, K. and Kittel, G. (2012). Climate change vulnerability and adaptation strategies for natural communities: Piloting methods in the Mojave and Sonoran deserts. (Report to the U.S. Fish and Wildlife Service.). Arlington, VA: NatureServe. Available: https://www.natureserve.org/publications/climate-change-vulnerability-and-adaptation-strategies-natural-communities-piloting.

Cross, M. S., Zavaleta, E. S. and Bachelet, D. *et al.* (2012) The Adaptation for Conservation Targets (ACT) framework: A tool for incorporating climate change into natural resource management. Environmental Management 50 (3), 341–351. https://doi.org/10.1007/s00267-012-9893-7.

Crowl, T. A., Crist, T. O., Parmenter, R. R., Belovsky, G. and Lugo, A. E. (2008) The spread of invasive species and infectious disease as drivers of ecosystem change. Frontiers in Ecology and the Environment 6 (5), 238–246.

D'Aloia, C. C., Naujokaitis-Lewis, I. and Blackford, C. *et al.* (2019) Coupled networks of permanent protected areas and dynamic conservation areas for biodiversity conservation under climate change. Frontiers in Ecology and Evolution 7, 27. https://doi.org/10.3389/fevo.2019.00027.

Davis, K. T., Dobrowski, S. Z. and Higuera, P. E. *et al.* (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proceedings of the National Academy of Sciences 116 (13), 6193–6198. https://doi.org/10.1073/pnas.1815107116.

Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C. and Mace, G. M. (2011) Beyond predictions: Biodiversity conservation in a changing climate. Science 332 (6025), 53–58. https://doi.org/10.1126/science.1200303.

DeGregorio, B. A., Westervelt, J. D., Weatherhead, P. J. and Sperry, J. H. (2015) Indirect effect of climate change: Shifts in ratsnake behavior alter intensity and timing of avian nest predation. Ecological Modelling 312, 239–246. https://doi.org/10.1016/j.ecolmodel.2015.05.031.

Descombes, P., Pitteloud, C. and Glauser, G. *et al.* (2020) Novel trophic interactions under climate change promote alpine plant coexistence. Science 370 (6523), 1469–1473. https://doi.org/10.1126/science.abd7015.

Diez, J. M., D'Antonio, C. M. and Dukes, J. S. *et al.* (2012) Will extreme climatic events facilitate biological invasions? Frontiers in Ecology and the Environment 10 (5), 249–257. https://doi.org/10.1890/110137.

Dormann, C. F. (2007) Promising the future? Global change projections of species distributions. Basic and Applied Ecology 8, 387–397.

Doyle, T. W., Krauss, K. W., Conner, W. H. and From, A. S. (2010) Predicting the retreat and migration of tidal forests along the northern Gulf of Mexico under sea-level rise. Adaptation of Forests and Forest Management to Changing Climate 259 (4), 770–777. https://doi.org/10.1016/j.foreco.2009.10.023.

Dudney, J., Hobbs, R. J., Heilmayr, R., Battles, J. J. and Suding, K. N. (2018) Navigating novelty and risk in resilience management. Trends in Ecology and Evolution 33 (11), 863–873. https://doi.org/10.1016/j.tree.2018.08.012.

Elliott, G. P. (2011) Influences of 20th-century warming at the upper tree line contingent on local-scale interactions: evidence from a latitudinal gradient in the Rocky Mountains, USA. Global Ecology and Biogeography 20 (1), 46–57.

Emmett, K. D., Renwick, K. M. and Poulter, B. (2021) Adapting a dynamic vegetation model for regional biomass, plant biogeography, and fire modeling in the Greater Yellowstone Ecosystem: Evaluating LPJ-GUESS-LMfireCF. Ecological Modelling 440, 109417. https://doi.org/10.1016/j.ecolmodel.2020.109417.

Engelhardt, E. K., Neuschulz, E. L. and Hof, C. (2020) Ignoring biotic interactions overestimates climate change effects: The potential response of the spotted nutcracker to changes in climate and resource plants. Journal of Biogeography 47 (1), 143–154. https://doi.org/10.1111/jbi.13699.

Escobar, L. E. and Craft, M. E. (2016) Advances and limitations of disease biogeography using ecological niche modeling. Frontiers in Microbiology 7, 1174.

Estay, S., Lima, M. and Labra, F. (2009) Predicting insect pest status under climate change scenarios: combining experimental data and population dynamics modelling. Journal of Applied Entomology 133 (7), 491–499.

Ettinger, A., Buonaiuto, D., Chamberlain, C., Morales-Castilla, I. and Wolkovich, E. (2021) Spatial and temporal shifts in photoperiod with climate change. New Phytologist 230 (2), 462–474.

Ettinger, A., Harvey, C. and Emmons, C. *et al.* (2022) Shifting phenology of an endangered apex predator mirrors changes in its favored prey. Endangered Species Research 48, 211–223.

Evans, M. E. K., Merow, C., Record, S., McMahon, S. M. and Enquist, B. J. (2016) Towards process-based range modeling of many species. Trends in Ecology and Evolution 31 (11), 860–871. https://doi.org/10.1016/j.tree.2016.08.005.

Fargione, J. E., Bassett, S. and Boucher, T. *et al.* (2018) Natural climate solutions for the United States. Science Advances 4 (11), 1869. https://doi.org/10.1126/sciadv.aat1869. (eaat).

Feehan, J., Harley, M. and van Minnen, J. (2009) Climate change in Europe. 1. Impact on terrestrial ecosystems and biodiversity. A review (reprinted). Agronomy for Sustainable Development 29 (3), 409–421.

Feeley, K. J. and Silman, M. R. (2010) Land-use and climate change effects on population size and extinction risk of Andean plants. Global Change Biology 16 (12), 3215–3222.

Fei, S., Desprez, J. M. and Potter, K. M. *et al.* (2017) Divergence of species responses to climate change. Science Advances 3 (5), e1603055. https://doi.org/10.1126/sciadv.1603055.

Fern, R. R., Morrison, M. L., Wang, H.-H., Grant, W. E. and Campbell, T. A. (2019) Incorporating biotic relationships improves species distribution models: Modeling the temporal influence of competition in conspecific nesting birds. Ecological Modelling 408, 108743. https://doi.org/10.1016/j.ecolmodel.2019.108743.

Fisichelli, N. A., Schuurman, G. W. and Hoffman, C. H. (2016) Is 'resilience' maladaptive? towards an accurate lexicon for climate change adaptation. Environmental Management 57 (4), 753–758. https://doi.org/10.1007/s00267-015-0650-6.

Fletcher Jr., R. J., Hefley, T. J. and Robertson, E. P. *et al.* (2019) A practical guide for combining data to model species distributions. Ecology 100 (6), e02710. https://doi.org/10.1002/ecy.2710.

Foden, W. and Young, B. (2016) IUCN SSC guidelines for assessing species' vulnerability to climate change. Cambridge: IUCN Species Survival Commission.

Foden, W. B., Butchart, S. H. M. and Stuart, S. N. *et al.* (2013) Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. PLOS ONE 8 (6), e65427. https://doi.org/10.1371/journal.pone.0065427.

Foden, W. B., Young, B. E. and Akçakaya, H. R. *et al.* (2019) Climate change vulnerability assessment of species. WIREs Climate Change 10 (1), e551. https://doi.org/10.1002/wcc.551.

Forrest, J. and Miller-Rushing, A. J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical transations of the Royal Society of London B 365 (1555), 3101–3112.

Franklin, J. F. and Lindenmayer, D. B. (2009) Importance of matrix habitats in maintaining biological diversity. Proceedings of the National Academy of Science of the United States of America 106, 349–350.

Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M. and Hargreaves, A. L. (2018) Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography 27 (11), 1268–1276. https://doi.org/10.1111/geb.12774.

Froeschke, G., Harf, R., Sommer, S. and Matthee, S. (2010) Effects of precipitation on parasite burden along a natural climatic gradient in southern Africa - implications for possible shifts in infestation patterns due to global changes. Oikos 119 (6), 1029–1039.

Game, E. T., Lipsett-Moore, G., Saxon, E., Peterson, N. and Sheppard, S. (2011) Incorporating climate change adaptation into national conservation assessments. Global Change Biology 17, 3150–3160.

Ganjurjav, H., Gornish, E. S. and Hu, G. *et al.* (2020) Warming and precipitation addition interact to affect plant spring phenology in alpine meadows on the central Qinghai-Tibetan Plateau. Agricultural and Forest Meteorology 287, 107943.

García Criado, M., Myers-Smith, I. H., Bjorkman, A. D., Lehmann, C. E. R. and Stevens, N. (2020) Woody plant encroachment intensifies under climate change across tundra and savanna biomes. Global Ecology and Biogeography 29 (5), 925–943. https://doi.org/10.1111/geb.13072.

Garrett, K. A., Dendy, S. P., Frank, E. E., Rouse, M. N. and Travers, S. E. (2006) Climate change effects on plant disease: Genomes to ecosystems. Annual Review of Phytopathology 44, 489–509.

Garrett, K. A., Nita, M. and De Wolf, E. D. *et al.* (2021) Chapter 24 – Plant pathogens as indicators of climate change. In: Letcher, T.M. (ed.) Climate Change (Third Edition). Elsevier, pp. 499–513. 10.1016/B978-0-12-821575-3.00024-4.

Geffroy, B. and Wedekind, C. (2020) Effects of global warming on sex ratios in fishes. Journal of Fish Biology 97 (3), 596–606.

Gehrig-Fasel, J., Guisan, A. and Zimmermann, N. E. (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment? Journal of Vegetation Science 18 (4), 571–582.

Gérard, M., Vanderplanck, M., Wood, T. and Michez, D. (2020) Global warming and plant–pollinator mismatches. Emerging Topics in Life Sciences 4 (1), 77–86. https://doi.org/10.1042/ETLS20190139.

Graham, N. A. J., Jennings, S., MacNeil, M. A., Mouillot, D. and Wilson, S. K. (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518 (7537), 94–97. https://doi.org/10.1038/nature14140.

Griscom, B. W., Adams, J. and Ellis, P. W. *et al.* (2017) Natural climate solutions. Proceedings of the National Academy of Sciences 114 (44), 11645–11650. https://doi.org/10.1073/pnas.1710465114.

Guo, F., Lenoir, J. and Bonebrake, T. C. (2018) Land-use change interacts with climate to determine elevational species redistribution. Nature Communications 9 (1), 1315. https://doi.org/10.1038/s41467-018-03786-9.

Hagerman, S., Satterfield, T. and Dowlatabadi, H. (2010) Climate change impacts, conservation and protected values: Understanding promotion, ambivalence and resistance to policy change at the World Conservation Congress. Conservation and Society 8 (4), 298–311.

Haines, A., Smith, K. R. and Anderson, D. *et al.* (2007) Energy and health 6 – Policies for accelerating access to clean energy, improving health, advancing development, and mitigating climate change. Lancet 370, 1264–1281.

Halpin, P. N. (1997) Global climate change and natural-area protection: Management responses and research directions. Ecological Applications 7 (3), 828–843.

Halsch, C. A., Shapiro, A. M. and Fordyce, J. A. *et al.* (2021) Insects and recent climate change. Proceedings of the national academy of Sciences 118 (2), e2002543117.

Hamann, E., Blevins, C., Franks, S. J., Jameel, M. I. and Anderson, J. T. (2021) Climate change alters plant–herbivore interactions. New Phytologist 229 (4), 1894–1910. https://doi.org/10.1111/nph.17036.

Hannah, L., Midgley, G. F. and Andelman, S. *et al.* (2007) Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5 (3), 131–138.

Hao, T., Elith, J., Guillera-Arroita, G. and Lahoz-Monfort, J. J. (2019) A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. Diversity and Distributions 25 (5), 839–852. https://doi.org/10.1111/ddi.12892.

Harris, J. A., Hobbs, R. J., Higgs, R. and Aronson, J. (2006) Ecological restoration and global climate change. Restoration Ecology 14 (2), 170–176.

Harris, R. M. B., Beaumont, L. J. and Vance, T. R. *et al.* (2018) Biological responses to the press and pulse of climate trends and extreme events. Nature Climate Change 8 (7), 579–587. https://doi.org/10.1038/s41558-018-0187-9.

Hayhoe, K., Cayan, D. and Field, C. B. *et al.* (2004) Emissions pathways, climate change, and impacts on California. PNAS 101 (34), 12422–12427.

Heller, N. E. and Zavaleta, E. S. (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142 (1), 14–32. https://doi.org/10.1016/j.biocon.2008.10.006.

Hellmann, J. J., Byers, J. E., Bierwagen, B. G. and Dukes, J. S. (2008) Five potential consequences of climate change for invasive species. Conservation Biology 22 (3), 534–543.

Henry, A. K. and Sorte, C. J. B. (2022) Impact assessment of coastal marine range shifts to support proactive management. Frontiers in Ecology and the Environment 20 (3), 161–169. https://doi.org/10.1002/fee.2447.

Higgins, P. A. T. (2007) Biodiversity loss under existing land use and climate change: An illustration using northern South America. Global Ecology and Biogeography 16 (2), 197–204.

Higgins, S. I., Larcombe, M. J., Beeton, N. J., Conradi, T. and Nottebrock, H. (2020) Predictive ability of a process-based versus a correlative species distribution model. Ecology and Evolution 10 (20), 11043–11054. https://doi.org/10.1002/ece3.6712.

Hobbs, R. J., Higgs, E. and Harris, J. A. (2009) Novel ecosystems: Implications for conservation and restoration. Trends in Ecology and Evolution 24 (11), 599–605.

Hockey, P. A. R., Sirami, C., Ridley, A. R., Midgley, G. F. and Babiker, H. A. (2011) Interrogating recent range changes in South African birds: Confounding signals from land use and climate change present a challenge for attribution. Diversity and Distributions 17 (2), 254–261.

Hoffmann, M., Hilton-Taylor, C. and Angulo, A. *et al.* (2010) The impact of conservation on the status of the world's vertebrates. Science 330 (6010), 1503–1509.

Hole, D. G., Willis, S. G. and Pain, D. J. *et al.* (2009) Projected impacts of climate change on a continent-wide protected area network. Ecology Letters 12 (5), 420–431.

Holling, C. S. (1978) Adaptive environmental assessment and management. New York, NY: Wiley.

Huang, W., Wang, W. and Cao, M. *et al.* (2021) Local climate and biodiversity affect the stability of China's grasslands in response to drought. Science of The Total Environment 768, 145482. https://doi.org/10.1016/j.scitotenv.2021.145482.

Hunter, M., Dinerstein, E., Hoekstra, J. and Lindenmayer, D. (2010) A call to action for conserving biological diversity in the face of climate change. Conservation Biology 24 (5), 1169–1171.

IPCC, (2007) Climate Change 2007: The physical science basis. In: Solomon, S., Qin, D., Manning, M., *et al.* (eds.) Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge and New York, NY: Cambridge University Press.

IPCC, (2014) Climate Change 2014: Impacts, adaptation, and vulnerability. Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

IPCC, (2021) Climate Change 2021: The physical basis. In: Masson-Delmotte, V., Zhai, P., Pirani, A., *et al.* (eds.) Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge Univeristy Press, p. 2391.

IPCC, (2022) Climate Change 2022: Impacts, adaptation, and vulnerability. In: Contribution of working group II to the sixth assessment report of the Intergovernmental Panel on Climate Change. Cambridge and New York, NY: Cambridge University Press. https://www.ipcc.ch/report/ar6/wg2/downloads/report/IPCC_AR6_WGII_FullReport.pdf.

Iwamura, T., Guzman-Holst, A. and Murray, K. A. (2020) Accelerating invasion potential of disease vector Aedes aegypti under climate change. Nature Communications 11 (1), 2130. https://doi.org/10.1038/s41467-020-16010-4.

Jack, D. W. and Kinney, P. L. (2010) Health co-benefits of climate mitigation in urban areas. Current Opinion in Environmental Sustainability 2, 172–177.

Jantz, S. M., Barker, B. and Brooks, T. M. *et al.* (2015) Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. Conservation Biology 29 (4), 1122–1131. https://doi.org/10.1111/cobi.12549.

Jaramillo, J., Chabi-Olaye, A. and Kamonjo, C. *et al.* (2009) Thermal tolerance of the coffee berry borer Hypothenemus hampei: Predictions of climate change impact on a tropical insect pest. PLOS ONE 4 (8), (Available: ://WOS:000268637700012).

Jarema, S. I., Samson, J., Mcgill, B. J. and Humphries, M. M. (2009) Variation in abundance across a species' range predicts climate change responses in the range interior will exceed those at the edge: A case study with North American beaver. Global Change Biology 15 (2), 508–522.

Jarnevich, C. S. and Stohlgren, T. J. (2009) Near term climate projections for invasive species distributions. Biological Invasions 11 (6), 1373–1379.

Jonsson, A. M., Harding, S., Barring, L. and Ravn, H. P. (2007) Impact of climate change on the population dynamics of Ips typographus in southern Sweden. Agricultural and Forest Meteorology 146 (1–2), 70–81.

Kareiva, P., Enquist, C. and Johnson, A. *et al.* (2008) Synthesis and conclusions. In: Julius, S.H., West, J.M. (eds.) Preliminary review of adaptation options for climate-sensitive ecosystems and resources. In a report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. Washington, D.C: Environmental Protection Agency. 9–1 to 9–66.

Kareiva, P., Daily, G., Ricketts, T., Tallis, H. and Polasky, S. (2011) Natural capital, theory and practice of mapping ecosystem services. Oxford university Press.

Keane, R. E., Holsinger, L. M., Parsons, R. A. and Gray, K. (2008) Climate change effects on historical range and variability of two large landscapes in western Montana, USA. Forest Ecology and Management 254 (3), 375–389.

Keane, R. E., Bentz, B., Holsinger, L. M., Saab, V. A. and Loehman, R. (2022) Modeled interactions of mountain pine beetle and wildland fire under future climate and management scenarios for three western US landscapes. Fire Ecology 18 (1), 12. https://doi.org/10.1186/s42408-022-00137-4.

Kearney, M. and Porter, W. (2009) Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. Ecology Letters 12 (4), 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x.

Keeler, A. M., Rose-Person, A. and Rafferty, N. E. (2021) From the ground up: Building predictions for how climate change will affect belowground mutualisms, floral traits, and bee behavior. Climate Change Ecology 1, 100013. https://doi.org/10.1016/j.ecochg.2021.100013.

Keith, D. A., Akçakaya, H. R. and Thuiller, W. *et al.* (2008) Predicting extinction risks under climate change: Coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters 4 (5), 560–563.

Kelly, L. T., Giljohann, K. M. and Duane, A. *et al.* (2020) Fire and biodiversity in the Anthropocene. Science 370 (6519), eabb0355. https://doi.org/10.1126/science.abb0355.

Kharouba, H. M. and Wolkovich, E. M. (2020) Disconnects between ecological theory and data in phenological mismatch research. Nature Climate Change 10 (5), 406–415. https://doi.org/10.1038/s41558-020-0752-x.

Kingsolver, J. G. and Buckley, L. B. (2018) How do phenology, plasticity, and evolution determine the fitness consequences of climate change for montane butterflies? Evolutionary applications 11 (8), 1231–1244.

Kohm, K. A. and Franklin, J. F. (1997) Creating a forestry for the 21st century: The science of ecosystem mangement. Washington, D.C: Island Press.

Kongsager, R. (2018) Linking climate change adaptation and mitigation: A review with evidence from the land-use sectors. Land 7 (4), 158. https://doi.org/10.3390/land7040158.

Krauss, K. W., From, A. S., Doyle, T. W., Doyle, T. J. and Barry, M. J. (2011) Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Islands region of Florida, USA. Journal of Coastal Conservation 15 (4), 629–638. https://doi.org/10.1007/s11852-011-0153-4.

Krosby, M., Theobald, D. M., Norheim, R. and McRae, B. H. (2018) Identifying riparian climate corridors to inform climate adaptation planning. PLOS ONE 13 (11), e0205156.

Lafferty, K. D. (2009) The ecology of climate change and infectious diseases. Ecology 90 (4), 888–900.

Lawler, J. J. (2009) Climate change adaptation strategies for resource management and conservation planning. Annals of the New York Academy of Sciences 1162, 79–98.

Lawler, J. J., Ruesch, A. S., Olden, J. D. and McRae, B. H. (2013) Projected climate-driven faunal movement routes. Ecology Letters 16 (8), 1014–1022.

Lawler, J. J., Ackerly, D. D. and Albano, C. M. *et al.* (2015) The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. Conservation Biology 29 (3), 618–629. https://doi.org/10.1111/cobi.12505.

Lawler, J. J., Rinnan, D. S. and Michalak, J. L. *et al.* (2020) Planning for climate change through additions to a national protected area network: implications for cost and configuration. Philosophical Transactions of the Royal Society B: Biological Sciences 375 (1794), 20190117. https://doi.org/10.1098/rstb.2019.0117.

Lendemer, J. C. and Allen, J. L. (2014) Lichen biodiversity under threat from sea-level rise in the Atlantic Coastal Plain. BioScience 64 (10), 923–931. https://doi.org/10.1093/biosci/biu136.

Littell, J. S., McKenzie, D., Peterson, D. L. and Westerling, A. L. (2009) Climate and wildfire area burned in western U. S. ecoprovinces, 1916-2003. Ecological Applications 19 (4), 1003–1021.

Littlefield, C. E., Krosby, M., Michalak, J. L. and Lawler, J. J. (2019) Connectivity for species on the move: Supporting climate-driven range shifts. Frontiers in Ecology and the Environment 17, 270–278.

Lobell, D. B. and Asner, G. P. (2003) Climate and management contributions to recent trends in U.S. agricultural yields. Science 299, 1032.

Lobell, D. B. and Field, C. B. (2007) Global scale climate-crop yield relationships and the impacts of recent warming. Environmental Research Letters 2, 14002–14007.

Locatelli, B., Pavageau, C., Pramova, E. and Di Gregorio, M. (2015) Integrating climate change mitigation and adaptation in agriculture and forestry: opportunities and trade-offs. WIREs Climate Change 6 (6), 585–598. https://doi.org/10.1002/wcc.357.

Lopera, D., Guo, K. C., Putman, B. J. and Swierk, L. (2022) Keeping it cool to take the heat: tropical lizards have greater thermal tolerance in less disturbed habitats. Oecologia 199 (4), 819–829. https://doi.org/10.1007/s00442-022-05235-3.

MacDonald, A. J., McComb, S., O'Neill, C., Padgett, K. A. and Larsen, A. E. (2020) Projected climate and land use change alter western blacklegged tick phenology, seasonal host-seeking suitability and human encounter risk in California. Global Change Biology 26 (10), 5459–5474.

Malevsky-Malevich, S. P., Molkentin, E. K., Nadyozhina, E. D. and Shklyarevich, O. B. (2008) An assessment of potential change in wildfire activity in the Russian boreal forest zone induced by climate warming during the twenty-first century. Climatic Change 86 (3–4), 463–474.

Malhi, Y., Aragao, L. and Galbraith, D. *et al.* (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Sciences of the United States of America 106 (49), 20610–20615.

Manning, A. D., Fischer, J. and Felton, A. *et al.* (2009) Landscape fluidity: A unifying perspective for understanding and adapting to global change. Journal of Biogeography 36 (2), 193–199.

Marlon, J. R., Bartlein, P. J. and Walsh, M. K. *et al.* (2009) Wildfire responses to abrupt climate change in North America. Proceedings of the National Academy of Sciences of the United States of America 106 (8), 2519–2524.

Marshall, L., Biesmeijer, J. C. and Rasmont, P. *et al.* (2018) The interplay of climate and land use change affects the distribution of EU bumblebees. Global Change Biology 24 (1), 101–116. https://doi.org/10.1111/gcb.13867.

Mas-Coma, S., Valero, M. A. and Bargues, M. D. (2009) Climate change effects on trematodiases, with emphasis on zoonotic fascioliasis and schistosomiasis. Veterinary Parasitology 163 (4), 264–280.

Mason, N. W. H., Ausseil, A.-G. E. and Dymond, J. R. *et al.* (2012) Will use of non-biodiversity objectives to select areas for ecological restoration always compromise biodiversity gains. Biological Conservation 155, 157–168. https://doi.org/10.1016/j.biocon.2012.05.019.

Matthews, A., Spooner, P. G., Lunney, D., Green, K. and Klomp, N. I. (2010) The influences of snow cover, vegetation and topography on the upper range limit of common wombats Vombatus ursinus in the subalpine zone, Australia. Diversity and Distributions 16 (2), 277–287. https://doi.org/10.1111/j.1472-4642.2010.00638.x.

Mawdsley, J. R., O'Malley, R. and Ojima, D. S. (2009) A Review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conservation Biology 23, 1080–1089.

Maxwell, S. L., Butt, N. and Maron, M. *et al.* (2019) Conservation implications of ecological responses to extreme weather and climate events. Diversity and Distributions 25 (4), 613–625. https://doi.org/10.1111/ddi.12878.

Mayor, S. J., Guralnick, R. P. and Tingley, M. W. *et al.* (2017) Increasing phenological asynchrony between spring green-up and arrival of migratory birds. Scientific Reports 7 (1), 1–10.

McClenachan, G., Witt, M. and Walters, L. J. (2021) Replacement of oyster reefs by mangroves: Unexpected climate-driven ecosystem shifts. Global Change Biology 27 (6), 1226–1238. https://doi.org/10.1111/gcb.15494.

McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A. and Theobald, D. M. (2016) Achieving climate connectivity in a fragmented landscape. Proceedings of the National Academy of Sciences 113 (26), 7195–7200. https://doi.org/10.1073/pnas.1602817113.

McLaughlin, B. C., Skikne, S. A. and Beller, E. *et al.* (2022) Conservation strategies for the climate crisis: An update on three decades of biodiversity management recommendations from science. BioScience 268, 109497.

McRae, B. H., Schumaker, N. H. and McKane, R. B. *et al.* (2008) A multi-model framework for simulating wildlife population response to land-use and climate change. Ecological Modelling 219 (1–2), 77–91.

Melles, S. J., Fortin, M.-J., Lindsay, K. and Badzinski, D. (2011) Expanding northward: Influence of climate change, forest connectivity, and population processes on a threatened species' range shift. Global Change Biology 17 (1), 17–31. https://doi.org/10.1111/j.1365-2486.2010.02214.x.

Menzel, A. (2005) A 500 year pheno-climatological view on the 2003 heatwave in Europe assessed by grape harvest dates. Meteorologische Zeitschrift ((Berlin)). 14.

Menzel, A. and Dose, V. (2005) Analysis of long-term time series of the beginning of flowering by Bayesian function estimation. Meteorologische Zeitschrift. 429–434.

Metzger, M. J., Schröter, D., Leemans, R. and Cramer, W. (2008) A spatially explicit and quantitative vulnerability assessment of ecosystem service change in Europe. Regional Environmental Change 8, 91–107.

Michalak, J. L., Lawler, J. J., Roberts, D. R. and Carroll, C. (2018) Distribution and protection of climatic refugia in North America. Conservation Biology 32 (6), 1414–1425. https://doi.org/10.1111/cobi.13130.

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. and Post, E. (2010) The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society B: Biological Sciences 365 (1555), 3177–3186.

Mina, M., Bugmann, H. and Cordonnier, T. *et al.* (2017) Future ecosystem services from European mountain forests under climate change. Journal of Applied Ecology 54 (2), 389–401. https://doi.org/10.1111/1365-2664.12772.

Mitchell, N. J., Allendorf, F. W., Keall, S. N., Daugherty, C. H. and Nelson, N. J. (2010) Demographic effects of temperature-dependent sex determination: Will tuatara survive global warming? Global Change Biology 16 (1), 60–72.

Moller, A. P. (2010) Host-parasite interactions and vectors in the barn swallow in relation to climate change. Global Change Biology 16 (4), 1158–1170.

Molnar, P. K., Derocher, A. E., Thiemann, G. W. and Lewis, M. A. (2010) Predicting survival, reproduction and abundance of polar bears under climate change. Biological Conservation 143 (7), 1612–1622.

Monsimet, J., Devineau, O., Pétillon, J. and Lafage, D. (2020) Explicit integration of dispersal-related metrics improves predictions of SDM in predatory arthropods. Scientific Reports 10 (1), 16668. https://doi.org/10.1038/s41598-020-73262-2.

Montesinos-Navarro, A., Estrada, A. and Font, X. *et al.* (2018) Community structure informs species geographic distributions. PLOS ONE 13 (5), e0197877. https://doi.org/10.1371/journal.pone.0197877.

Mora, C., McKenzie, T. and Gaw, I. M. *et al.* (2022) Over half of known human pathogenic diseases can be aggravated by climate change. Nature Climate Change 12 (9), 869–875. https://doi.org/10.1038/s41558-022-01426-1.

Morelli, T. L., Daly, C. and Dobrowski, S. Z. *et al.* (2016) Managing climate change refugia for climate adaptation. PLOS ONE 11 (8), e0159909. https://doi.org/10.1371/journal.pone.0159909.

Morin, C. W. and Comrie, A. C. (2010) Modeled response of the West Nile virus vector Culex quinquefasciatus to changing climate using the dynamic mosquito simulation model. International Journal of Biometeorology 54 (5), 517–529.

Morin, X., Viner, D. and Chuine, I. (2008) Tree species range shifts at a continental scale: New predictive insights from a process-based model. Journal of Ecology 96, 784–794.

Neil, K. L., Landrum, L. and Wu, J. G. (2010) Effects of urbanization on flowering phenology in the metropolitan phoenix region of USA: Findings from herbarium records. Journal of Arid Environments 74 (4), 440–444.

Nitschke, C. R. and Innes, J. L. (2008) Climatic change and fire potential in South-Central British Columbia, Canada. Global Change Biology 14 (4), 841–855.

Nobis, M. P., Jaeger, J. A. G. and Zimmermann, N. E. (2009) Neophyte species richness at the landscape scale under urban sprawl and climate warming. Diversity and Distributions 15 (6), 928–939.

Nolan, C., Overpeck, J. T. and Allen, J. R. M. *et al.* (2018) Past and future global transformation of terrestrial ecosystems under climate change. Science 361 (6405), 920–923. https://doi.org/10.1126/science.aan5360.

Nordic Council of Ministers, 2017. Mitigation and Adaptation Synergies in the NDCs. Denmark: Nordic Council of Ministers. doi: 10.6027/TN2017–524.

Nuñez, T. A., Lawler, J. J. and McRae, B. H. *et al.* (2013) Connectivity planning to address climate change. Conservation Biology 27 (2), 407–416. https://doi.org/10.1111/cobi.12014.

Oakes, L. E., Cross, M. S. and Zavaleta, E. S. (2021) Rapid assessment to facilitate climate-informed conservation and nature-based solutions. Conservation Science and Practice 3 (8), e472. https://doi.org/10.1111/csp2.472.

O'Connor, T. G., Puttick, J. R. and Hoffman, M. T. (2014) Bush encroachment in southern Africa: changes and causes. African Journal of Range and Forage Science 31 (2), 67–88. https://doi.org/10.2989/10220119.2014.939996.

Ogden, N. H., Bigras-Poulin, M. and Hanincova, K. *et al.* (2008) Projected effects of climate change on tick phenology and fitness of pathogens transmitted by the North American tick Ixodes scapularis. Journal of Theoretical Biology 254 (3), 621–632.

Olwoch, J. M., Reyers, B. and van Jaarsveld, A. S. (2009) Host-parasite distribution patterns under simulated climate: implications for tick-borne diseases. International Journal of Climatology 29 (7), 993–1000.

Ooi, M. K., Auld, T. D. and Denham, A. J. (2009) Climate change and bet-hedging: Interactions between increased soil temperatures and seed bank persistence. Global Change Biology 15 (10), 2375–2386.

Ovaskainen, O., Tikhonov, G. and Norberg, A. *et al.* (2017) How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters 20 (5), 561–576. https://doi.org/10.1111/ele.12757.

Ozgul, A., Childs, D. Z. and Oli, M. K. *et al.* (2010) Coupled dynamics of body mass and population growth in response to environmental change. Nature 466 (7305), 482–485.

Pacifici, K., Reich, B. J. and Miller, D. A. W. *et al.* (2017) Integrating multiple data sources in species distribution modeling: A framework for data fusion. Ecology 98 (3), 840–850. https://doi.org/10.1002/ecy.1710.

Pacifici, M., Rondinini, C. and Rhodes, J. R. *et al.* (2020) Global correlates of range contractions and expansions in terrestrial mammals. Nature Communications 11 (1), 2840. https://doi.org/10.1038/s41467-020-16684-w.

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

Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Parmesan, C., Ryrholm, N. and Stefanescu, C. *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399, 579–583.

Patz, J. A., Gibbs, H. K., Foley, J. A., Rogers, J. V. and Smith, K. R. (2007) Climate change and global health: Quantifying a growing ethical crisis. Ecohealth 4 (4), 397–405.

Patz, J. A., Olson, S. H., Uejio, C. K. and Gibbs, H. K. (2008) Disease emergence from global climate and land use change. Medical Clinics of North America 92 (6), 1473–1491.

Pearson, R. G. and Dawson, T. P. (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.

Pearse, W. D., Davis, C. C., Inouye, D. W., Primack, R. B. and Davies, T.J. 2017. A statistical estimator for determining the limits of contemporary and historic phenology. Nature Ecology and Evolution. 1 (12), 1876+. https://doi.org/10.1038/s41559-017-0350-0.

Pecl, G. T., Araújo, M. B. and Bell, J. D. *et al.* (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355 (6332), eaai9214. https://doi.org/10.1126/science.aai9214.

Peers, M. J. L., Majchrzak, Y. N. and Menzies, A. K. *et al.* (2020) Climate change increases predation risk for a keystone species of the boreal forest. Nature Climate Change 10 (12), 1149–1153. https://doi.org/10.1038/s41558-020-00908-4.

Peters, R. L. and Darling, J. D. S. (1985) The greenhouse effect and nature reserves: Global warming would diminish biological diversity by causing extinctions among reserve species. BioScience 35 (11), 707–717.

Peterson, E. K., Jones, C. D. and Sandmeier, F. C. *et al.* (2021) Drought influences biodiversity in a semi-arid shortgrass prairie in southeastern Colorado. Journal of Arid Environments 195, 104633. https://doi.org/10.1016/j.jaridenv.2021.104633.

Peterson St-Laurent, G., Oakes, L. E., Cross, M. and Hagerman, S. (2021) R-R-T (resistance–resilience–transformation) typology reveals differential conservation approaches across ecosystems and time. Communications Biology 4 (1), 1–9. https://doi.org/10.1038/s42003-020-01556-2.

Phillips, B. L., Kelehear, C. and Pizzatto, L. *et al.* (2010) Parasites and pathogens lag behind their host during periods of host range advance. Ecology 91 (3), 872–881.

Piao, S., Liu, Q. and Chen, A. *et al.* (2019) Plant phenology and global climate change: Current progresses and challenges. Global Change Biology 25 (6), 1922–1940. https://doi.org/10.1111/gcb.14619.

Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M. and Hartig, F. (2020) Machine learning algorithms to infer trait-matching and predict species interactions in ecological networks. Methods in Ecology and Evolution 11 (2), 281–293. https://doi.org/10.1111/2041-210X.13329.

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L. and Levin, S. A. (2013) Marine taxa track local climate velocities. Science 341, 1239–1242.

Podur, J. and Wotton, M. (2010) Will climate change overwhelm fire management capacity? Ecological Modelling 221 (9), 1301–1309.

Pokhriyal, P., Rehman, S. and Areendran, G. *et al.* (2020) Assessing forest cover vulnerability in Uttarakhand, India using analytical hierarchy process. Modeling Earth Systems and Environment 6 (2), 821–831. https://doi.org/10.1007/s40808-019-00710-y.

Polley, L. and Thompson, R. C. A. (2009) Parasite zoonoses and climate change: Molecular tools for tracking shifting boundaries. Trends in Parasitology 25 (6), 285–291.

Poloczanska, E. S., Brown, C. J. and Sydeman, W. J. *et al.* (2013) Global imprint of climate change on marine life. Nature Climate Change 3 (10), 919.

Ponti, L., Cossu, Q. A. and Gutierrez, A. P. (2009) Climate warming effects on the Olea europaea–Bactrocera oleae system in Mediterranean islands: Sardinia as an example. Global Change Biology 15 (12), 2874–2884. https://doi.org/10.1111/j.1365-2486.2009.01938.x.

Powers, R. P. and Jetz, W. (2019) Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nature Climate Change 9 (4), 323–329. https://doi.org/10.1038/s41558-019-0406-z.

Price, S. J., Leung, W. T. M. and Owen, C. J. *et al.* (2019) Effects of historic and projected climate change on the range and impacts of an emerging wildlife disease. Global Change Biology 25 (8), 2648–2660. https://doi.org/10.1111/gcb.14651.

Prober, S. M., Doerr, V. A. J., Broadhurst, L. M., Williams, K. J. and Dickson, F. (2019) Shifting the conservation paradigm: A synthesis of options for renovating nature under climate change. Ecological Monographs 89 (1), e01333. https://doi.org/10.1002/ecm.1333.

Pyke, C. R. and Fischer, D. T. (2005) Selection of bioclimatically representative biological reserve systems under climate change. Biological Conservation 121 (3), 429–441.

Radinger, J., Hölker, F. and Horký, P. *et al.* (2016) Synergistic and antagonistic interactions of future land use and climate change on river fish assemblages. Global Change Biology 22 (4), 1505–1522. https://doi.org/10.1111/gcb.13183.

Rafferty, N. E. (2017) Effects of global change on insect pollinators: Multiple drivers lead to novel communities. Current Opinion in Insect Science 23, 22–27. https://doi.org/10.1016/j.cois.2017.06.009.

Rapacciuolo, G., Maher, S. P. and Schneider, A. C. *et al.* (2014) Beyond a warming fingerprint: Individualistic biogeographic responses to heterogeneous climate change in California. Global Change Biology 20 (9), 2841–2855. https://doi.org/10.1111/gcb.12638.

Regos, A., Hermoso, V., D'Amen, M., Guisan, A. and Brotons, L. (2018) Trade-offs and synergies between bird conservation and wildfire suppression in the face of global change. Journal of Applied Ecology 55 (5), 2181–2192. https://doi.org/10.1111/1365-2664.13182.

Renner, S. S. and Zohner, C. M. (2018) Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annual Review of Ecology, Evolution, and Systematics 49 (1), 165–182.

Rilov, G., David, N. and Guy-Haim, T. *et al.* (2021) Sea level rise can severely reduce biodiversity and community net production on rocky shores. Science of the Total Environment 791, 148377. https://doi.org/10.1016/j.scitotenv.2021.148377.

Rose, H., Caminade, C. and Bolajoko, M. B. *et al.* (2016) Climate-driven changes to the spatio-temporal distribution of the parasitic nematode, Haemonchus contortus, in sheep in Europe. Global Change Biology 22 (3), 1271–1285. https://doi.org/10.1111/gcb.13132.

Rosenthal, J. (2009) Climate change and the geographic distribution of infectious diseases. Ecohealth 6 (4), 489–495.

Ruthrof, K. X., Breshears, D. D. and Fontaine, J. B. *et al.* (2018) Subcontinental heat wave triggers terrestrial and marine, multi-taxa responses. Scientific Reports 8 (1), 13094. https://doi.org/10.1038/s41598-018-31236-5.

Schleuning, M., Neuschulz, E. L. and Albrecht, J. *et al.* (2020) Trait-based assessments of climate-change impacts on interacting species. Trends in Ecology and Evolution 35 (4), 319–328. https://doi.org/10.1016/j.tree.2019.12.010.

Schloss, C. A., Nuñez, T. A. and Lawler, J. J. (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences 109 (22), 8606–8611. https://doi.org/10.1073/pnas.1116791109.

Schröter, D., Cramer, W. and Leemans, R. *et al.* (2005) Ecosystem service supply and vulnerability to global change in Europe. Science 310 (5752), 1333–1337. https://doi.org/10.1126/science.1115233.

Schulte to Bühne, H., Tobias, J. A., Durant, S. M. and Pettorelli, N. (2021) Improving predictions of climate change–land use change Interactions. Trends in Ecology and Evolution 36 (1), 29–38. https://doi.org/10.1016/j.tree.2020.08.019.

Schuurman, G. W., Cole, D. N. and Cravens, A. E. *et al.* (2022) Navigating ecological transformation: Resist–accept–direct as a path to a new resource management paradigm. BioScience 72 (1), 16–29. https://doi.org/10.1093/biosci/biab067.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S. and Kühn, I. (2008) Climate change can cause spatial mismatch of trophically interacting species. Ecology 89 (12), 3472–3479. https://doi.org/10.1890/07-1748.1.

Schweiger, O., Biesmeijer, J. C. and Bommarco, R. *et al.* (2010) Multiple stressors on biotic interactions: How climate change and alien species interact to affect pollination. Biological Reviews 85 (4), 777–795.

Seddon, N., Chausson, A. and Berry, P. *et al.* (2020) Understanding the value and limits of nature-based solutions to climate change and other global challenges. Philosophical Transactions of the Royal Society B: Biological Sciences 375 (1794), 20190120. https://doi.org/10.1098/rstb.2019.0120.

Segan, D. B., Murray, K. A. and Watson, J. E. M. (2016) A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. Global Ecology and Conservation 5, 12–21. https://doi.org/10.1016/j.gecco.2015.11.002.

Sillmann, J., Thorarinsdottir, T. and Keenlyside, N. *et al.* (2017) Understanding, modeling and predicting weather and climate extremes: Challenges and opportunities. Weather and Climate Extremes 18, 65–74. https://doi.org/10.1016/j.wace.2017.10.003.

Smith, P., Arneth, A. and Barnes, D. K. A. *et al.* (2022) How do we best synergize climate mitigation actions to co-benefit biodiversity? Global Change Biology 28 (8), 2555–2577. https://doi.org/10.1111/gcb.16056.

Snall, T., Benestad, R. E. and Stenseth, N. C. (2009) Expected future plague levels in a wildlife host under different scenarios of climate change. Global Change Biology 15 (2), 500–507.

Sorte, C. J. B., IbÃ¡Ã±ez, I. and Blumenthal, D. M. *et al.* (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecology Letters 16 (2), 261–270.

Spence, A. R. and Tingley, M. W. (2020) The challenge of novel abiotic conditions for species undergoing climate-induced range shifts. Ecography 43 (11), 1571–1590. https://doi.org/10.1111/ecog.05170.

Stein, B. A., Staudt, A. and Cross, M. S. *et al.* (2013) Preparing for and managing change: Climate adaptation for biodiversity and ecosystems. Frontiers in Ecology and the Environment 11 (9), 502–510. https://doi.org/10.1890/120277.

Stein, B. A., Glick, P., Edelson, N. A. and Staudt, A. (2014). Climate-smart conservation: Putting adaptation principles into practice. Washington, D.C.: National Wildlife Federation. Available: www.nwf.org/ClimateSmartGuide.

Storkey, J., Stratonovitch, P., Chapman, D. S., Vidotto, F. and Semenov, M. A. (2014) A process-based approach to predicting the effect of climate change on the distribution of an invasive allergenic plant in Europe. PLOS ONE 9 (2), e88156. https://doi.org/10.1371/journal.pone.0088156.

Stralberg, D., Carroll, C. and Pedlar, J. H. *et al.* (2018) Macrorefugia for North American trees and songbirds: Climatic limiting factors and multi-scale topographic influences. Global Ecology and Biogeography 27 (6), 690–703. https://doi.org/10.1111/geb.12731.

Strange, N., Thorsen, B. J., Bladt, J., Wilson, K. A. and Rahbek, C. (2011) Conservation policies and planning under climate change. Biological Conservation 144 (12), 2968–2977. https://doi.org/10.1016/j.biocon.2011.08.022.

Sun, Q., Li, B., Jiang, Y., Chen, X. and Zhou, G. (2021) Declined trend in herbaceous plant green-up dates on the Qinghai–Tibetan Plateau caused by spring warming slowdown. Science of the Total Environment 772, 145039.

Swanston, C., Janowiak, M., Brandt, L. and Handler, S. (2016). Forest adaptation resources: Climate change tools and approaches for land managers, 2nd edition. Gen. Tech. Rep. NRS-GTR-87–2, p. 161. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. doi: 10.2737/NRS-GTR-87-2.

Swart, R. and Raes, F. (2007) Making integration of adaptation and mitigation work: Mainstreaming into sustainable development policies? Integrating Climate Change Actions Into Local Development. Routledge. pp. 288–303.

Thackeray, S. J., Sparks, T. H. and Frederiksen, M. *et al.* (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16 (12), 3304–3313.

Thomas, M. B. (2020) Epidemics on the move: Climate change and infectious disease. PLOS Biology 18 (11), e3001013. https://doi.org/10.1371/journal.pbio.3001013.

Thomas, C. D., Anderson, B. J. and Moilanen, A. *et al.* (2013) Reconciling biodiversity and carbon conservation. Ecology Letters 16 (s1), 39–47. https://doi.org/10.1111/ele.12054.

Thompson, L. M., Lynch, A. J. and Beever, E. A. *et al.* (2021) Responding to ecosystem transformation: Resist, accept, or direct? Fisheries 46 (1), 8–21. https://doi.org/10.1002/fsh.10506.

Thorne, J. H., Choe, H. and Stine, P. A. *et al.* (2018a) Climate change vulnerability assessment of forests in the Southwest USA. Climatic Change 148 (3), 387–402. https://doi.org/10.1007/s10584-017-2010-4.

Thorne, K., MacDonald, G. and Guntenspergen, G. *et al.* (2018b) U.S. Pacific coastal wetland resilience and vulnerability to sea-level rise. Science Advances 4 (2), eaao3270. https://doi.org/10.1126/sciadv.aao3270.

Thurman, L. L., Stein, B. A. and Beever, E. A. *et al.* (2020) Persist in place or shift in space? Evaluating the adaptive capacity of species to climate change. Frontiers in Ecology and the Environment 18 (9), 520–528. https://doi.org/10.1002/fee.2253.

Tikhonov, G., Opedal, Ø.H. and Abrego, N. *et al.* (2020) Joint species distribution modelling with the r-package Hmsc. Methods in Ecology and Evolution 11 (3), 442–447. https://doi.org/10.1111/2041-210X.13345.

Tobin, P. C., Nagarkatti, S., Loeb, G. and Saunders, M. C. (2008) Historical and projected interactions between climate change and insect voltinism in a multivoltine species. Global Change Biology 14 (5), 951–957.

Traill, L. W., Lim, M. L. M., Sodhi, N. S. and Bradshaw, C. J. A. (2010) Mechanisms driving change: Altered species interactions and ecosystem function through global warming. Journal of Animal Ecology 79 (5), 937–947. https://doi.org/10.1111/j.1365-2656.2010.01695.x.

Trebicki, P. (2020) Climate change and plant virus epidemiology. Virus Research 286, 198059. https://doi.org/10.1016/j.virusres.2020.198059.

United Nations Environment Programme, (2021). Guidelines for integrating ecosystem-based adaptation into national adaptation plans: Supplement to the UNFCCC NAP technical guidelines. Available: https://wedocs.unep.org/20.500.11822/36703.

Urban, M. C. (2020) Climate-tracking species are not invasive. Nature Climate Change 10 (5), 382–384. https://doi.org/10.1038/s41558-020-0770-8.

Verlinden, M. and Nijs, I. (2010) Alien plant species favoured over congeneric natives under experimental climate warming in temperate Belgian climate. Biological Invasions 12 (8), 2777–2787.

Vörösmarty, C. J., Green, P., Salisbury, J. and Lammers, R. B. (2000) Global water resources: Vulnerability from climate change and population growth. Science 289 (5477), 284–288. https://doi.org/10.1126/science.289.5477.284.

Vos, C. C., Berry, P. and Opdam, P. *et al.* (2008) Adapting landscapes to climate change: Examples of climate-proof ecosystem networks and priority adaptation zones. Journal of Applied Ecology 45 (6), 1722–1731.

Walker, B. (2020) Resilience: What it is and is not. Ecology and Society 25 (2), 11. https://doi.org/10.5751/ES-11647-250211.

Wallingford, P. D., Morelli, T. L. and Allen, J. M. *et al.* (2020) Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. Nature Climate Change 10 (5), 398–405. https://doi.org/10.1038/s41558-020-0768-2.

Walters, C. J. and Hilborn, R. (1978) Ecological optimization and adaptive management. Annual Review of Ecology and Systematics 9, 157–188.

Watson, J. E. M. (2014) Human responses to climate change will seriously impact biodiversity conservation: It's time we start planning for them. Conservation Letters 7 (1), 1–2. https://doi.org/10.1111/conl.12083.

Watson, J. E. M., Evans, T. and Venter, O. *et al.* (2018) The exceptional value of intact forest ecosystems. Nature Ecology and Evolution 2 (4), 599–610. https://doi.org/10.1038/s41559-018-0490-x.

Weiskopf, S. R., Rubenstein, M. A. and Crozier, L. G. *et al.* (2020) Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. Science of the Total Environment 733, 137782. https://doi.org/10.1016/j.scitotenv.2020.137782.

Wernberg, T., Bennett, S. and Babcock, R. C. *et al.* (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353 (6295), 169–172. https://doi.org/10.1126/science.aad8745.

Williams, J. W., Ordonez, A. and Svenning, J.-C. (2021) A unifying framework for studying and managing climate-driven rates of ecological change. Nature Ecology and Evolution 5 (1), 17–26. https://doi.org/10.1038/s41559-020-01344-5.

Williams, P. H., Hannah, L. and Andelman, S. J. *et al.* (2005) Planning for climate change: Identifying minimum-dispersal corridors for the Cape Proteaceae. Conservation Biology 19 (4), 1063–1074.

Willis, C. G., Ruhfel, B. R. and Primack, R. B. *et al.* (2010) Favorable climate change response explains non-native species' success in Thoreau's Woods. PLOS ONE 5 (1), (Available: ://000273896500007).

Wilsey, C. B., Lawler, J. J. and Maurer, E. P. *et al.* (2013) Tools for assessing climate impacts on fish and wildlife. Journal of Fish and Wildlife Management 4 (1), 220–241. https://doi.org/10.3996/062012-JFWM-055.

Wolkovich, E., Auerbach, J. and Chamberlain, C. *et al.* (2021) A simple explanation for declining temperature sensitivity with warming. Global Change Biology 27 (20), https://doi.org/10.1111/gcb.15746.

Yates, C. J., Elith, J. and Latimer, A. M. *et al.* (2010) Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: Opportunities and challenges. Austral Ecology 35 (4), 374–391. https://doi.org/10.1111/j.1442-9993.2009.02044.x.

Yu, H., Luedeling, E. and Xu, J. (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. Proceedings of the National Academy of Sciences 107 (51), 22151–22156.

Further Reading

Hagerman, S., Dowlatabadi, H., Satterfield, T. and McDaniels, T. (2010) Expert views on biodiversity conservation in an era of climate change. Global Environmental Change 20 (1), 192–207. https://doi.org/10.1016/j.gloenvcha.2009.10.005.