REVIEW PAPER



Managing biodiversity under climate change: challenges, frameworks, and tools for adaptation

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Abstract The myriad challenges facing biodiversity under climate change are reflected in the challenges facing managers planning for these impacts. An ever-expanding number of recommendations and tools for climate change adaptation exist to aid managers in these efforts, yet navigating these various resources can lead to information overload and paralysis in decision-making. Here we provide a synthesis of the key considerations, approaches, and available tools for integrating climate change adaptation into management plans. We discuss principal elements in climate change adaptation-incorporating uncertainty through scenario planning and adaptive management—and review three leading frameworks for incorporating climate change adaptation into place-based biodiversity conservation planning. Finally, we identify the following key questions needed for longterm conservation planning and review the associated tools and techniques needed to address them: (1) How is the climate projected to change in my study area?; (2) How are non-climatic stressors projected to change?; (3) How vulnerable are species to climate change impacts?; (4) How are species ranges likely to respond?; and (5) How are management strategies expected to affect outcomes? In doing so, we aim to aid natural resource managers in navigating the burgeoning field of climate change adaptation planning and provide managers a roadmap for managing biodiversity under climate change.

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Introduction

Natural resource managers are faced with the challenge of incorporating climate change adaptation strategies into management plans as the effects of climate change on biodiversity are becoming increasingly evident. Over the next century, species and ecosystems are expected to respond to a wide range of climate-related effects, many of which have already been observed. In response to changing climate, species are shifting their phenology by changing the timing of life history events such as blooming, migration, and breeding (Parmesan and Matthews 2005). In the second half of the twentieth century, for example, warmer spring temperatures across the United States have led to earlier timing of the breeding season of tree swallows (Dunn and Winkler 1999). In addition, species are also changing in space by shifting their ranges and distributions. Range shifts have been observed in response to temperature and precipitation changes in the Sierra Nevada for birds (Tingley et al. 2012), butterflies (Forister et al. 2010), and small mammals (Moritz et al. 2008; Rowe et al. 2014) over the last 100 years. Moreover, significant range contractions (>80%) are predicted to occur for up to 2/3 of the native flora in California, USA, while other species are predicted to experience range expansions (Loarie et al. 2008; Thorne et al. 2016). For species with poor dispersal ability and specialized habitat requirements, such as amphibian populations threatened by loss of wetlands (Lowe 2012; Ryan et al. 2014), climate change can lead to local or even global extinction (Thomas et al. 2004).

Composite and indirect effects of climate change, such as exotic species invasions, will also likely compound impacts on ecological communities. A classic example is the combined effects of warming winters, which allow multiple broods of native bark beetles (Coleoptera: Curculionidae, Scolytinae) to emerge, and increased occurrence of severe drought, rendering trees more susceptible to bark beetles (Bentz et al. 2010). These climate-induced effects have led to changes in tree stand communities in the western United States and Canada (Bentz et al. 2010). Increased temperatures have also been linked with the spread of harmful pathogens, such as the fungus *Batrachochytrium dendrobatidis* causing alarming declines in amphibian populations (Bosch et al. 2007; Padgett-Flohr and Hopkins 2010). Taken together, these effects may scale up to changes in entire community structure resulting in novel ecosystems (Hobbs et al. 2009). These ecosystem-level changes need not be far off; in California, for instance, assemblages of breeding bird communities without any analogue to those existing in the present day are expected to be seen in the next several decades (Stralberg et al. 2009).

The myriad challenges facing biodiversity under climate change are now reflected in the challenges facing managers in planning for these effects. Traditionally, the focus of conservation work has been on protecting and managing systems to maintain their current state or restore degraded systems back to a historical state (Jackson and Hobbs 2009). Under climate change, not only have the threats to biodiversity changed, but also the habitat or species assemblage being managed may very well be different in the future (Bellard et al. 2012). Conventional conservation strategies are insufficient in this new era; working within preserve borders and population boundaries to conserve existing species and habitats as a steady-state system could lead to wasted energy and opportunities (Stein et al. 2014). Conserving "the stage" is still a helpful concept, but the stage is changing, and a "no

analog" future may mean that restoration to a past reference state may be futile (Hobbs et al. 2009). The manager is now faced with a moving target; setting interim goals and adaptively managing for ecosystems in transition are increasingly becoming new challenges. Moreover, there is now a need to consider broader approaches both in terms of geography and time. With realized and potential shifting of species ranges and intensified competition with human uses for water and habitats across landscapes, a greater diversity of jurisdictions and sectors will need to adopt shared goals and cooperate despite their potentially conflicting priorities (Leck and Simon 2013).

The conservation community has largely embraced the fact that addressing the effects of climate change requires new approaches to resource management. Managers and conservationists are diligently working to understand new kinds of information and speak the language of this new science with climate scientists, policy-makers, and each other. There have been advances in guidance in the form of principles and frameworks for developing climate change adaptation strategies, and now there are many examples of applications of these processes, which are as diverse as the resources being managed (Heller and Zavaleta 2009; Groves et al. 2012; Stein et al. 2013). However, developing adaptation plans for a specific preserve or resource remains challenging. Resource managers are required to draw upon available, often sparse, data to describe the drivers of change and types and severity of effects that are locally relevant. Climate adaptation planners need help to find and interpret the science and also know how much data are enough to allow confidence in moving forward. Difficulties arise from the complexity of climate science and need to plan around the uncertainties of climate change in the future. Climate change projection data are highly technical and there are many models to compare when attempting to predict the range of possibilities that the future may hold (Daniels et al. 2012). Moreover, compounding uncertainty in both bioclimatic models and climate change projections can lead to different and sometimes even contradictory predictions of species' future range shifts (Thuiller 2004). To the non-climate scientist, talk of uncertainty may appear to throw all potential actions into doubt. Together, these challenges can lead to information overload and paralysis in decision-making.

To aid natural resource managers in navigating this burgeoning field, we synthesize principal elements of climate change adaptation, frameworks for applying these principles, and available tools and techniques to address key management questions. Based on our geographic expertise many of the examples we provide are drawn from California; however, the lessons learned are broadly applicable to any geographic region. In addition, we present case studies highlighting successful applications of frameworks specifically proposed for incorporating climate change adaptation into place-based biodiversity conservation planning.

Principal elements of climate change adaptation

Climate change adaptation is the process of modifying one's strategies to persist and succeed under new and changing climate conditions. This can refer to adaptation by a species in the evolutionary sense, but for this discussion we are focused on the efforts of the resource manager and what the Intergovernmental Panel on Climate Change (IPCC) describes as "initiatives and measures to reduce the vulnerability of natural and human systems against actual or expected climate change effects" (IPCC 2007). In other words, climate adaptation may be thought of as preparing for, coping with, or adjusting to climatic changes and their associated impacts (Stein et al. 2013). Yet what does this mean in

practice? Here we review two principal elements to climate change adaptation—incorporating uncertainty and adaptive management.

Incorporating uncertainty

Uncertainty refers to incomplete knowledge either from a lack of information, disagreement about what is known, or because what is being studied itself may be unknowable (IPCC 2014). Uncertainty may arise from imprecision in the data, ambiguously defined concepts or terminology, or uncertain projections of human behavior, and thus, can be measured both quantitatively or qualitatively (IPCC 2014). In climate change adaptation, sources of uncertainty occur at multiple stages throughout the process, including uncertainty in climate change projections (magnitude and direction of change), species or ecosystem responses to climate change, and consequences of management actions (Stein et al. 2014). Given these ambiguities, decision-making can prove a tremendous challenge.

A wide variety of types of uncertainty that can impact decision-making have been identified. Within climate science, researchers have distinguished between structural uncertainty, referring to the functional forms of the models (i.e., which processes are modeled and what the equations are), and parametric uncertainty, referring to the value of empirical quantities (Morgan 2009; Parker 2014). Within ecology, a distinction has been drawn between epistemic uncertainty and linguistic uncertainty (Regan et al. 2002; Elith et al. 2002). Epistemic uncertainty refers to uncertainty about a determinant fact, and includes categories such measurement error, systematic error, and model uncertainty. Linguistic uncertainty arises from the fact that much of natural language is ambiguous, vague, or underspecified. As an example, counting the number of mature plants in a population runs into the difficulty of linguistic vagueness because some plants are on the borderline between being fully mature and juvenile (Elith et al. 2002).

A best-practices approach for incorporating uncertainty in climate change adaptation planning and management is scenario planning (Peterson et al. 2003). Scenario planning provides a framework in which multiple plausible futures are used to evaluate the outcomes and consequences of different decisions that need to be made under multiple scenarios that capture the range of uncertainties. Most scenario planning begins by identifying highly uncertain but driving factors for a system. Factors that have a certainty associated with direction and magnitude of change are detailed and assumed across all plausible future scenarios. Planners then develop quantitative or qualitative scenarios about the state of the uncertain factors in the future. These scenarios provide story lines for evaluating the performance of different decisions under the alternative futures. For example, recommended management strategies for protecting native flora and fauna under different scenarios of climate change have included reducing non-climatic stressors like invasive species removal (Ryan et al. 2014), protecting or restoring climate microrefugia such as riparian zones (Loarie et al. 2008; Seavy et al. 2009), or in extreme scenarios assisted migration (Vitt et al. 2010; Gray et al. 2011).

The ultimate ambition of scenario planning is developing management actions that would perform well under multiple scenarios, such that the outcomes are robust to the uncertainty in future conditions (Wilby and Dessai 2010). The U.S. Forest Service, for example, strongly encourages managers to explore a range of possible climate scenarios to identify management strategies that could help ensure resilience of natural resources across a broad set of potential conditions (Daniels et al. 2012). Scenario planning can also be used to brainstorm novel management options and formulate flexible long-term plans. Finally, the strategy of taking a scenario-neutral approach, in other words not trying to assess the

likelihood of different hazards, can lead to outcomes that are more robust to uncertainty (Prudhomme et al. 2010).

Adaptive management

Once a management decision has been made and an action implemented, adaptive management is important for refining and adjusting management prescriptions as new information is gleaned or if monitoring suggests a different approach might be better suited (Williams and Brown 2012). Adaptive management involves an iterative process of implementing a management action, monitoring, and assessment to inform future decisionmaking (Williams and Brown 2012). An effective monitoring regime is central to this process, as it allows for the comparison of management outcomes with the outcomes predicted to occur. Monitoring involves the identification of status indicators that measure short-and long-term changes in natural resources, establishment of baseline data for future comparisons, and development of a monitoring protocol specifying the timing and frequency of data collection (Parma 1998). Once data are collected through monitoring, they are assessed to determine whether the management action is meeting its objectives. This evaluation is then applied in future management decision-making.

Adaptive management addresses the fact that natural systems can rarely be fully understood, and that there is value in monitoring the responses of resources to learn from different management actions (Williams and Brown 2012). This becomes especially important when managers are dealing with uncertainty and rapidly changing conditions. It also provides the added benefit of gaining further information about the environmental system itself, by perturbing it with a management action and observing its response. Adaptive management is most effective in an experimental context, where a sampling design for different management strategies can be implemented, monitored, and statistically evaluated. In practice, however, adaptive management is sometimes reduced to 'reactive management', where apparently unsuccessful management strategies are altered or abandoned unsystematically. Thus, a criticism of adaptive management is that it lends itself to weak conservation (Sutherland 2006). True adaptive management requires a structured, iterative approach that is often time- or resource-consuming, and may not provide results in the timeframe needed for management decisions. On the other hand, it is argued that the urgency of global climate change means that adaptation actions must be taken immediately, requiring that implementation and adjustment of management approaches occur simultaneously (Hansen et al. 2010). Because of its dynamic and learning-based approach, adaptive management is typically a key component in frameworks for climate change adaptation, and should be implemented with as much experimental structure as realistically possible.

Frameworks for adaptation

Several frameworks for climate change adaptation exist, though few are targeted specifically for land managers managing for biodiversity conservation. Here we compare, contrast and provide case studies for the three most widely applied or cited frameworks developed for in situ natural resource management according to an ISI Web of Science search for the following terms: TS = (climate adaptation and biodiversity) and TI = (framework*).

'Adaptation for conservation targets' framework

The Adaptation for Conservation Targets (ACT) framework offers a structured approach for developing specific adaptation actions that explicitly incorporate the principles of scenario planning and adaptive management to address uncertainty (Cross et al. 2012b). The framework delineates six steps to climate change adaptation: (1) identify the conservation feature of interest and define conservation objectives, (2) build a conceptual model to assess impacts of possible future scenarios, (3) identify management options, (4) prioritize actions, (5) implement actions, and (6) monitor and evaluate outcomes (Fig. S1). The development of a conceptual model is a strong feature of the framework as it reveals the climatic, ecological, social, and economic mechanisms behind anticipated climate change impacts. By identifying these drivers, users of the framework can more specifically evaluate how they might change under different climate change scenarios, and more robustly predict how the species, habitat, or ecosystem may respond under each scenario. One of the framework's key contributions is its reliance on local knowledge and expert opinion in developing the conceptual model. While expert opinion may not replace the role of quantitative data, in the common case that appropriate data are not available, this process allows for a time- and cost-effective alternative that is well suited to involve a breadth of stakeholders.

The ACT framework has been implemented in a number of cases across North America (Cross et al. 2012a). As a specific example, in 2012 the Wildlife Conservation Society Canada, in partnership with the Kresge Foundation, organized a workshop to determine climate change vulnerabilities of freshwater fish in Ontario's Far North and identify potential adaptation actions to support decision-making (Wildlife Conservation Society 2013). Participants in the workshop included representatives from provincial government ministries, First Nations communities, research organizations, and academic institutions. After identifying three key watersheds in which to focus management efforts for freshwater fish species, participants were asked to develop a conceptual model to illustrate the physical, ecological, social, and climate drivers of freshwater fish populations. They identified climate stressors such as water temperature, ice cover, and fire regimes, and nonclimate stressors such as fishing and hydro-development, as major drivers. Participants evaluated how these drivers may change under the IPCC A2 high emissions future climate scenario for the three watersheds and resulting potential effects on freshwater fish such as losses in habitat and coldwater species. Participants then identified intervention points based on the conceptual model where there were opportunities for influencing outcomes, and brainstormed potential adaptation options for reducing vulnerabilities, thus achieving the objectives of the workshop.

'Climate-smart conservation' framework

The Climate-Smart Conservation (CSC) framework similarly offers a structured approach to integrate climate-change adaptation and adaptive management into already existing planning processes (Stein et al. 2014). In comparison with the ACT framework, the CSC framework does not explicitly call for developing a conceptual model to evaluate potential climate change impacts, though this may be incorporated into the vulnerability assessment stage of the CSC framework. However, it features an important additional step, which is to re-evaluate and potentially adjust the conservation objective(s) of the plan in light of assessing climate change vulnerabilities. The CSC framework's seven-step approach to

climate change adaptation is therefore: (1) define conservation objectives, (2) identify key climate vulnerabilities, (3) revise objectives as necessary, (4) identify management options, (5) prioritize actions, (6) implement actions, and (7) monitor and evaluate outcomes (Fig. S2). Thus, in this framework the conservation goals, and not just the management strategies, may be shifted when considering climate change impacts.

While the CSC framework has been widely implemented (Stein et al. 2014), we highlight one example here. In 2012 and 2013, the U.S. Forest Service (USFS) in collaboration with EcoAdapt and the California Landscape Conservation Cooperative initiated the Climate Change Adaptation Project for the Sierra Nevada, California. The project aimed to determine climate change vulnerabilities of key Sierra Nevada resources and identify management strategies to prioritize actions for adaptation (Kershner 2014a). Its first step was identification of focal resources and management goals, which were the conservation of a range of ecosystem types (e.g., mixed conifer systems) and flora and fauna species (e.g., yellow-legged frogs [Rana muscosa]). Based on future climate, wildfire, hydrology, and vegetation projections for the Sierra Nevada, project participants provided expert opinions of high, moderate, or low vulnerability scores for each focal resource (Kershner 2014b). Experts also ranked their confidence in these values as high, moderate, or low to incorporate uncertainty. Given these vulnerabilities, participants reassessed the management goals for each focal resource for challenges, opportunities, and feasibility. They then brainstormed possible adaptation actions, such targeted stand thinning, use of prescribed burning, invasive species removal, species reintroductions, and protecting climate microrefugia. To prioritize actions, each participant ranked their top five actions to prioritize for each focal resource. Finally, participants worked in groups to develop implementation plans for prioritized actions, specifying the location and timeframe for action, resources needed, and potential partners. Results from this effort are informing revisions to the USFS Forest Management Plans, the revision of the California State Wildlife Action Plan, as well as several other natural resource agencies and organizations management planning efforts.

'Portfolio decision analysis' framework

The Portfolio Decision Analysis (PDA) framework offers an altogether different approach from the ACT or CSC frameworks, in that it provides a quantitative methodology for selecting a portfolio of management actions specifically where there is a direct trade-off between human activities and biodiversity conservation (Convertino and Valverde 2013). The approach is analogous to optimizing financial portfolios, where natural resources and the built environment are considered natural and human assets, respectively, and allocation of management actions are optimized to maximize natural assets while minimizing impact to human assets. The value of each asset varies over time as a function of climate conditions (e.g., level of sea level rise, drought) and management actions. Specific details on the optimization algorithm are provided in Convertino and Valverde (2013), but the general steps of the PDA framework are: (1) identify natural and human assets of interest, (2) determine vulnerabilities of and risks to assets, (3) identify potential management actions, (4) quantify the 'effectiveness' value of management actions, (5) determine costs of management actions, and (6) determine an optimal set of management actions given costs and budget constraints (Fig. S3). The framework accounts for uncertainty by integrating different predictions of policy impacts, ecosystem responses, and climate scenarios into determining the vulnerabilities of assets.

The PDA framework was developed in the context of natural resource management on U.S. military lands, and is best applied wherever there is conflict between human land use and biodiversity management. An early example of the approach's application was in the management of Santa Rosa Island (SRI), Florida, which is an installation of Eglin Air Force Base (Convertino and Valverde 2013). SRI sits at the northern boundary of the Gulf of Mexico, and contains critical habitat for the state-listed endangered Snowy Plover (Charadrius nivosus). SRI is also used for military activities like training and recreation. Both the natural and human assets of concern on SRI are threatened by sea-level rise. The PDA framework was applied to optimize conservation of land for military mission and preserve the habitat of Snowy Plovers and other migratory shorebirds. The process used GIS-based biophysical models to inform predictions of risks to assets given sea-level rise. The SRI installation was gridded into management-scale areas, and a Multi Criteria Decision Analysis model was used to calculate 'effectiveness' values for protecting Snowy Plover habitat for different management actions within each area. Finally, the PDA optimization model identified target areas for habitat restoration that maximized the value of assets across the entire installation. The Santa Rosa Island case study found that the PDA approach identified the most efficient set of actions that maximized environmental benefits and either held equal or minimized costs as compared with other decision-making approaches (Convertino and Valverde 2013).

Tools and techniques to address key management questions

To apply climate change adaptation frameworks successfully, a number of questions must be answered along the way. Here we discuss key questions needed for long-term conservation planning, and associated tools and techniques to address them (Table 1). Throughout each of the following stages, the question '*What are the uncertainties*?' should be considered and addressed via scenario planning and data-driven adaptive management.

How is the climate projected to change in my study area?

The vast majority of climate change projections rely on mathematical models of the circulation of the Earth's atmosphere and ocean, termed general circulation models (GCMs). Atmospheric and oceanic GCMs are key components of global climate models along with sea ice and land-surface components. Because the scale of a GCM output is coarse—a grid cell from a typical GCM model run being $2.5^{\circ} \times 2.5^{\circ}$ or roughly 250 km²— it is difficult to use GCM output directly in most regional and local-scale environmental modeling. Rather, it is necessary to downscale the GCM output: that is, to add information to the model so that it has a finer spatial resolution. The two general strategies for downscaling are dynamical downscaling, in which physical meteorological processes are directly modeled at a finer spatial scale, or statistical downscaling, in which a spatial interpolation algorithm is applied to interpolate course climate data to finer scales (Daniels et al. 2012). Because dynamical downscaling is computationally intensive, it is not often used for climate projections, especially for those that are multi-decadal in time scale or incorporate multiple models (Table 1).

Question	Tool	GeoFocus	Variables	Resolution Source	Source
How is the climate projected to change?	Climate Wizard	Global	Precipitation Average temperature	12 km	http://www.climatewizard.org/
	WorldClim	Global	Precipitation Max. temperature Min. temperature Bioclimatic variables	900 m	http://www.worldclim.org/cmip5_30s
	ClimateData	U.S.	Precipitation Max. temperature Min. temperature	800 m	http://www.climatedata.us/
	California Basin Characterization Model	California	Precipitation Max. temperature Min. temperature Climate water deficit Potential evapotranspiration Actual evapotranspiration Recharge Runoff April 1 snowpack	270 m	http://climate.calcommons.org/dataset/2014- CA-BCM

Table 1 continued					
Question	Tool	GeoFocus	Variables	Resolution	Source
How are non-climate stressors projected to change?	National Land Cover Database	U.S.	Land cover Percent developed impervious Percent canopy cover Land cover change	30 m	http://www.mrlc.gov/
	USGS Anthropogenic Land Use Trends, 1974-2012	U.S.	Land cover Housing unit density Mining/ extraction/forestry Change in cultivated lands Change in protected lands	60 m	http://landsat.gsfc.nasa.gov/?p=11044
	CalWeedMapper	California	Invasive species occurrence	15 km	http://calweedmapper.cal-ipc.org/
How vulnerable is this species?	Climate Change Vulnerability Index	U.S.	Projected temp. change Projected precip. change Landscape context Natural history traits	N/A	http://www.natureserve.org/conservation-tools/ climate-change-vulnerability-index
	System for Assessing Vulnerability of Species	Global	Projected habitat change Natural history traits	N/A	http://www.fs.fed.us/rm/grassland-shrubland- desert/products/species-vulnerability/
	Climate Change Sensitivity Database	U.S.	Physiology Life history Habitat Dispersal ability Ecology	N/A	http://www.climatechangesensitivity.org

Table 1 continued					
Question	Tool	GeoFocus	Variables	Resolution	Source
How is the species range likely MaxEnt to respond?	MaxEnt	User-defined	Species occurrence User's choice of environmental and climatic variables	User- defined	http://www.cs.princeton.edu/~ schapire/ maxent/
	Gap Analysis Program Species Viewer	U.S.	Species occurrence Land cover Percent canopy cover Human disturbance Slope Aspect Elevation Distance to forest edge Distance to ecotone Hydrography	30 m	http://gapanalysis.usgs.gov/species/viewer/
	Climate Change Atlas	U.S.	Species occurrence Average temperature Precipitation Elevation	20 km	http://www.fs.fed.us/nrs/atlas/
	OceanAdapt	U.S. marine areas	Species occurrence Latitude Depth Sea surface temperature Sea bottom temperature	100 km	http://oceanadapt.rutgers.edu/

Table 1 continued					
Question	Tool	GeoFocus	Variables	Resolution Source	Source
How will management strategies affect outcomes?	NatureServe Vista	User-defined	User's choice	User- defined	http://www.natureserve.org/conservation-tools/ natureserve-vista
	Coastal Resilience	N. America coastal regions	Land Cover Land use Infrastructure Human population Habitat change Sea level rise Storm and flood impacts	Varied	http://maps.coastalresilience.org/network/
	Marxan	User-defined	User's choice	User- defined	http://www.uq.edu.au/marxan/
	Zonation	User-defined	User's choice	User- defined	http://cbig.it.helsinki.fl/software/zonation/

An extensive list of resources for global, U.S. and California extents can be found at www.climate.calcommons.org

How are non-climate stressors projected to change in my study area?

In addition to examining how climate is projected to change in a region, it is valuable to consider how non-climate stressors such as habitat conversion, fragmentation, and species invasions may affect species' vulnerability (Klausmeyer et al. 2011). Non-climatic stressors can both be exacerbated by climate change, such as in the case of increased tree mortality caused by bark beetles under warming temperatures (Bentz et al. 2010), as well as exacerbate climate change impacts on species, such as habitat fragmentation impeding species from tracking their climatic niche and shifting ranges (Robillard et al. 2015). To predict secondary impacts that may occur in a system, it is informative to assess the region's trajectories of land-use and land cover change (Theobald 2014; Homer et al. 2015). However, extending historical trajectories into the future is a highly uncertain exercise, hence scenario planning approaches are warranted here.

How vulnerable are species to climate change impacts?

Assessment of vulnerability to climate change is the analysis of the extent to which a species, habitat, or ecosystem is susceptible to impacts from climate change (Lankford et al. 2014). Assessing vulnerability can help prioritize which species may require greater management resources, identify intervention points for leveraging action, and reconsider conservation goals in light of climate change (Young et al. 2014). Most forms of vulnerability assessments involve the analysis of three principal components: sensitivity, exposure, and adaptive capacity of the species or system under question (Glick et al. 2011). Sensitivity refers to how tolerant the species or system is to changes in environmental factors like temperature or precipitation, and often is represented by physiological or life history traits of the species in question. Exposure refers to the degree to which the species or system will actually experience a given type of change in its environment. Adaptive capacity refers to the ability of the species or system to cope with environmental changes with minimal disruption (Glick et al. 2011). Many types of vulnerability assessments exist; they can be quantitative or qualitative, such as binning organisms into categories of low, moderate, or high vulnerability, and can be conducted at the level of species, habitat, and ecosystem. Because of these variations, it is important to be conscientious of the goal of the assessment when choosing an assessment method (Lankford et al. 2014). In some cases, the data availabilities and requirements of an assessment method may limit which assessments are even possible. A recommended rule of thumb is to evaluate vulnerabilities with more than one assessment to compare outputs (Lankford et al. 2014).

How are species ranges likely to respond?

An important analytical technique in determining predicted range shifts is developing species distribution models. Species distribution models (SDMs), among other uses, can help predict the locations of rare and threatened plant and animal species, model the potential spread of invasive species, and provide a comprehensive set of distribution maps that can be used in conservation prioritization. In the context of climate change, species distribution modeling can be used to generate predictions of suitable habitat assuming the species' niche has migrated in geographical space with the change in climate (Ramirez-Villegas et al. 2014). A workflow for many types of species distribution modeling involves assembling a stack of relevant environmental variables, collecting a species observation

dataset, developing a statistical model expressing the relationship between known observations and environmental variables, and then mapping the predicted probability of occurrence to geographical space (Guisan and Thuiller 2005). Types of environmental variables may include climate, topography, edaphic factors, land use, the distributions of other species, and disturbances. Uncertainty in SDM predictions should be considered by exploring the sensitivity of the models to different variable weighting schemes and cut-off values for probabilities of occurrence (Thuiller 2004). Evaluating the results of the distribution model is an important final step in producing a model (Porfirio et al. 2014). This is accomplished through visual inspection of maps of the model's output, assessment of the ecological plausibility of the key environmental variables identified in the model, and statistical tests that make use of known occurrence points that have been set aside for comparison. A number of species distribution maps and user-friendly statistical tools (e.g., MaxEnt) for generating distributions of unmapped taxa are freely available online (Table 1). Techniques in species distribution modeling continue to evolve, for instance by incorporating species co-occurrence likelihoods, thus enhancing our ability to model range shifts in species assemblages (Pollock et al. 2014; Harris 2015).

How are management strategies expected to affect outcomes?

Spatially explicit analysis tools are powerful instruments for comparing the outcomes of potential management strategies and supporting decision-making. These tools take as input spatial data on environmental and socioeconomic factors, and allow users to evaluate different management scenarios based on user-defined criteria like economic cost versus conservation benefit (Moilanen et al. 2009). Spatial analysis tools developed for reserve design like Marxan or Zonation can also aid land trusts and government landowners in prioritizing lands for acquisition as part of their climate change adaptation strategy. Some spatial analysis software programs integrate with Geographic Information Systems and allow users to have a high level of control of the program's variable inputs and outputs (e.g., Marxan, Zonation, NatureServe Vista). These tools offer great flexibility and predictive capacity, but require users to acquire all data layers themselves and rely on relatively high analytical expertise of the user (Watts et al. 2009; Lehtomäki and Moilanen 2013). In contrast, other spatial analysis tools offer web-based explorers that are more user-friendly and include built-in datasets, but are therefore less customizable (e.g., Coastal Resilience; Table 1).

Conclusions

Managing biodiversity under climate change can seem insurmountably complex, but a great deal of work exists showing that natural resource managers can feasibly incorporate climate change adaptation into their planning. Here we have provided a synthesis of the central elements and frameworks for climate change adaptation, examples of their implementation, and tools to address key questions needed for long-term conservation planning. While it is important to consider the types and range of changes that could occur, it is not necessary to have a perfect crystal ball to predict the future to make good management decisions. Underpinning the climate change adaptation process is the explicit consideration of uncertainty in decision-making and the course-corrections provided by monitoring and re-evaluation, which taken together in an adaptive management approach

support defensible action. By adopting a common terminology for navigating this process and sharing challenges and successes, natural resource managers can pave the way for forward-looking adaptive management to become the new status quo.

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