Approaches to Evaluating Climate Change Impacts on Species: A Guide to Initiating the Adaptation Planning Process

Erika L. Rowland · Jennifer E. Davison · Lisa J. Graumlich

Received: 29 March 2010/Accepted: 23 December 2010 © Springer Science+Business Media, LLC 2011

Abstract Assessing the impact of climate change on species and associated management objectives is a critical initial step for engaging in the adaptation planning process. Multiple approaches are available. While all possess limitations to their application associated with the uncertainties inherent in the data and models that inform their results, conducting and incorporating impact assessments into the adaptation planning process at least provides some basis for making resource management decisions that are becoming inevitable in the face of rapidly changing climate. Here we provide a non-exhaustive review of long-standing (e.g., species distribution models) and newly developed (e.g., vulnerability indices) methods used to anticipate the response to climate change of individual species as a guide for managers grappling with how to begin the climate change adaptation process. We address the limitations (e.g., uncertainties in climate change projections) associated with these methods, and other considerations for matching appropriate assessment approaches with the management questions and goals. Thorough consideration of the objectives, scope, scale, time frame and available resources for a climate impact assessment allows for informed method selection. With many data sets and tools available on-line, the capacity to undertake and/or benefit

E. L. Rowland $(\boxtimes) \cdot J$. E. Davison \cdot L. J. Graumlich School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, USA e-mail: erowland@wcs.org

J. E. Davison · L. J. Graumlich College of the Environment, University of Washington, Seattle, WA 98195, USA

E. L. Rowland Wildlife Conservation Society, Bozeman, MT 59715, USA from existing species impact assessments is accessible to those engaged in resource management. With some understanding of potential impacts, even if limited, adaptation planning begins to move toward the development of management strategies and targeted actions that may help to sustain functioning ecosystems and their associated services into the future.

Keywords Climate change · Vulnerability assessments · Management · Species · Adaptation planning

Introduction

Multiple lines of evidence point to widespread impacts of warming temperatures and climatic extremes on species and ecosystem processes, prompting natural resource practitioners to look for ways to incorporate the threat of this exacerbating stressor into management planning. In recent years numerous papers have outlined broad-spectrum strategies for adaptation, which we define as human actions intended to reduce the biophysical impacts of climate change, to address this pressing issue (e.g., Millar and others 2007; Baron and others 2009; Mawdsley and others 2009; Lawler and others 2010a; Hansen and others 2010). The critical precursor to identifying appropriate adaptation strategies for natural resources is to assess the potential impacts of climate change on conservation targets and on the outcomes of existing management in order to develop and modify management actions and allocate resources (West and others 2009). Given the availability of multiple approaches and the uncertainties associated with climate projections and models for forecasting species' responses, starting the process may seem daunting.

Initiating engagement in this first step in the adaptation process, some managers have undertaken impact assessments at varying levels of biological organization, from species and taxonomic groups (e.g., Peterson and others 2002; Lawler and others 2009) to vegetation communities and ecosystems (e.g., Hamann and Wang 2006; Enquist and Gori 2008; Loarie and others 2009). In this article we focus on long-standing as well as newly developed methods used by scientists and managers to anticipate the response to climate change of individual species for which they hold stewardship mandates or conservation interest. Potential impacts of climate change on species characterize their vulnerability; as used here, vulnerability is a function of both a species' inherent sensitivity to and exposure to changing climate (Williams and others 2008; West and others 2009). Sensitivity is defined by species' traits, including morphology, physiology, life history, dispersal and behavior, all of which govern response to abiotic habitat conditions. Also important are biotic interactions that regulate response, for example the dependence on other species for habitat creation or services such as pollination. Exposure refers to an organism's experience of the effects of climate change in its physical habitat, and also includes indirect influence manifest through changes in important processes (e.g., disturbance regimes), shifts in vegetation structure and composition, or impacts on coastal environments through sea-level fluctuation (Fig. 1). An organism may be directly exposed to climate by, for example, changes in temperature, precipitation, the length of the growing season, and the frequency of extreme events. Because a species may be inherently sensitive to changes in climate but not be exposed to such changes, or exposed to climate change but not sensitive, both are important to consider in vulnerability assessments. It is also important to keep in mind that, regardless of a species' climate-related vulnerability, there are numerous non-climate factors, such as land use changes and the spatial distribution of anthropogenic barriers (e.g., dams, urban areas, transportation corridors) that can impair its inherent ability (i.e., adaptive capacity) to respond to climate conditions.

Approaches to assessing species' vulnerability to climate change can be categorized into two broad groups. First, there are examinations of spatially explicit shifts in the geographical range of species with changing climate. These may be based on empirical evidence from the paleoecological record of past changes in response to Holocene climate cycles (e.g., Guralnick 2007) or twentieth century observations of shifts in species (Parmesan and Yohe 2003; Rosenzweig and others 2008). Future range changes may also be forecast using species distribution models (SDMs), based either on correlative associations with environmental variables (e.g., Thuiller and others

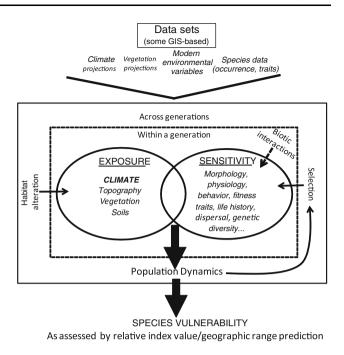


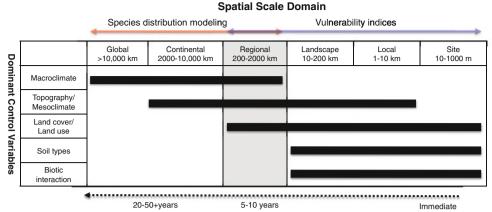
Fig. 1 Factors associated with sensitivity and exposure considered in species vulnerability assessments (Modified from Kearney and Porter 2009)

2005; Pearson and others 2006; Lawler and others 2009) or on mechanistic relationships between species and their environments (e.g., Kearney and Porter 2009). The second group of assessment approaches employs evaluative frameworks that generate relative indices of climate change vulnerability. These indices integrate information about species' exposure and sensitivity to climate change based on observation, field experiments and the results of SDMs, if available.

In the following sections we more fully describe the approaches in these two broad categories of vulnerability assessment as reported in the literature, both peer-reviewed journals and reports. We also address the limitations and uncertainties associated with these methods, and other considerations for matching appropriate assessment approaches with the management applications or questions. In doing so, we hope to provide a non-exhaustive review that serves as a guide for managers grappling with how to begin the climate change adaptation process.

Detailing the Approaches

An understanding of the key elements of the various vulnerability assessments is important for selecting an appropriate approach or set of approaches on which to base adaptation planning (Table 1). In this section we first discuss the Holocene and twentieth century observations of species distribution dynamics, followed by descriptions of



Temporal Scale: Management Decision/Planning Horizon

Fig. 2 Matrix for evaluating the suitability of the vulnerability assessment approaches to key elements of project scope (Modified from Pearson and Dawson 2003)

Table 1 Summary of vulnerability assessment approaches including assumptions, examples of insights, and requirements for application

Approach	Critical assumptions	Insights to date	Information requirements	References
Observational	impact assessment			
Paleoecology	Rates and patterns of change over last 1000 to 10,000 years offer insights into regional and multi-decadal scale processes	allowing species to track climate change	Pollen or macrofossil records and/or proxy data (some rich data archives exist)	Huntley 1991; Grayson 2005; Guralnick 2007
		 Topographic barriers prevent species movements 		
		• Species respond individualistically to climate		
Twentieth century observations	Recent rates and patterns are guide to future	• Differing controls at upper elevation vs. lower elevation boundaries and poleward vs. equatorial limits	Systematic historical collections for part/all of the twentieth century (some rich data archives exist)	Merrill and others 2008; Rowe and others 2010; Myers and others 2009
		• Provides robust evidence for detection of current climate impacts		
		• Response rates can be rapid when thresholds are crossed		
Species distrik	pution models			
Bioclimatic envelope models	Correlation between current distribution and current climate offers ability to forecast future	• Projected species range shifts can highlight vulnerable species and the role of habitat connectivity, providing broad scale guidance to direct conservation efforts	Robust data on species ranges (occurrence) and associated climate conditions	Lawler and others 2010a, b; Pearson and Dawson 2003
Mechanistic species distribution models	Physiological tolerances and functional traits linked to energy balance equations are key factors limiting distribution	• Projected species ranges include suitable habitat not represented by current distribution, likely expanding range forecasts into novel climate conditions anticipated for the future	Robust data on physiological tolerances of species to key climatic variables	Kearney and Porter 2009; Monahan 2009
Vulnerability i	indices			
Vulnerability indices	Species factors related to biotic interactions, dispersal and habitat needs are important elements of vulnerability at local to regional scales	• Relative vulnerability of multiple species point to overlapping sources of vulnerability and potential management efficiencies	Detailed data about the biology and ecology of multiple species	Young and others 2009; Finch and others 2011; US EPA 2009
		• Land use/management influence vulnerability assessment results		

The data required for many approaches are available for a limited number of species

species distribution modeling. We end with a presentation of three recently developed climate change vulnerability indices.

Documenting and Forecasting Changes in Species Geographic Distributions

Observations from the twentieth century and the paleoecological record of past climatic change are two sources of information for assessing potential future impacts on species (Willis and Birks 2006). While the rate and magnitude of twenty-first century warming is likely to produce climate states with no known analogs (Williams and others 2007), some limited understanding of species' responses may be gleaned from warmer-than-present climatic periods during the Holocene, namely the Medieval warm period (ca. AD 950-1250) and changes from the post-glacial through the mid-Holocene (ca. 7000-5000 years ago). Pollen and macrofossils preserved in sediments and packrat middens yield paleoecological records of vegetation response. Reconstructions from these data point to key mechanisms behind vegetation range shifts, such as longdistance dispersal to initiate colonization, and multi-decadal variability in climatic extremes to facilitate population expansion and contraction (e.g., Gray and others 2006; MacDonald and others 2008). In addition, reconstructions of post-glacial vegetation response provide rough estimates of migration rates, albeit through landscapes with negligible anthropogenic modification, which suggests that these may overestimate twenty-first century rates (e.g., Huntley 1991; Jackson and Booth 2002). Paleoecology has also demonstrated the important role of climate refugia for some species during past periods of climate change (e.g., Schauffler and Jacoboson 2002; Gray and others 2006). In addition, fossil-based evidence of range shifts in animal species exists. In one example, Grayson (2005) reconstructed the late-Quaternary shifts in the distribution of American pika (Ochotona princpes) in response to changing climate conditions. Other studies have examined the Holocene response of mammals throughout North America, as well as the effects of topographic heterogeneity on migration rates (Graham and others 1996; Guralnick 2007).

Several reviews have compiled worldwide examples of twentieth century shifts in the spatial distributions of both plant and animal species, representing a second source of observation-based analysis of species distribution dynamics (e.g., Walther and others 2002; Parmesan and Yohe 2003; Root and others 2003; Rosenzweig and others 2008). Accounts at varying spatial scales continue to appear in the literature, documenting range contractions and expansions at distributional limits. For example, some species of birds in North America are moving their winter ranges northward (Niven and others 2009), as well as shifting breeding distributions to higher elevations (Tingley and others 2009). Similar trends have been documented for small mammal species at latitudinal margins (Myers and others 2009) and along elevational gradients (Beever and others 2003; Moritz and others 2008). Not limited to vertebrates, recent climate responses have also been observed in insect species (e.g., Parmesan and others 1999; Chen and others 2009) and plants (e.g., Kelly and Goulden 2008). Other instructive studies have documented more complicated responses to climate change, involving differing controls over upper and lower range limits, and other factors, namely land use and existing anthropogenic stressors (Parmesan 2006; Moritz and others 2008; Merrill and others 2008; Rowe and others 2010). Many observational studies provide insights into the potentially rapid rate at which changes in species distributions can occur, and sometimes identify driving mechanisms or key climate variables behind these changes.

Species distribution models (SDMs) offer an alternative approach to observation-based vulnerability assessment, providing forecasts with an explicit spatial component. While applications of SDMs to questions about constraints on species' distributions are numerous, their use as a tool to forecast species' responses to changing climate is increasingly prevalent (e.g., Lawler and others 2006). In creating SDMs, relationships between species and the environmental variables that are thought to limit current ranges are modeled to examine potential future ranges with environmental change (Pearson and Dawson 2003; Guisan and Thuiller 2005; Kearney and Porter 2009). With the advent of geographic information systems (GIS) and spatially explicit data sets, the range of climatic conditions that constrain species' distributions can be combined with geo-referenced projections from climate models to generate maps of potential changes in species' distributions-alluringly invaluable products for management applications.

Species distribution models for predicting responses to climate change may be correlative or mechanistic in approach (Hijmans and Graham 2006; Kearney and Porter 2009). Both correlative and mechanistic models are based in niche theory that attributes constraints on species' occurrence to sets of environmental conditions and interactions with other organisms (Wiens and others 2009). Also referred to as niche models, mechanistic and correlative SDMs are underpinned by different manifestations of niche: fundamental and realized niche, respectively (Guisan and Thuiller 2005; Wiens and others 2009). Fundamental niche describes the full set of environmental conditions in which a species may exist, the entire scope of which is effectively never known for any species. Mechanistic models represent fundamental niche by using species functional traits, principally physiological tolerances and exchanges of energy and mass related to climatic conditions, to model species distributions (Kearney and Porter 2009). Mechanistic models are developed from theoretical energy balance equations, as well as experimental and field-based observations of physiological tolerances (e.g., Kearney and others 2008; Monahan 2009). These data are independent of species known geographic ranges. The resulting models project all areas of potentially suitable habitat, less the influence of dispersal limitations, complex biotic interactions inherent in species occurrence records, and the influence of disturbance and other ecosystem processes (Kearney and Porter 2009; Monahan 2009).

The realized niche is a subset of the fundamental niche of a species and is represented by the observed distribution of a species as constrained by biotic interactions (e.g., competition, predation, pollination) and disturbances (including land use). Correlative SDMs, typically called bioclimatic envelope models, approximate the realized niche of a species by deriving statistical relationships between species' occurrence records and a set of environmental variables, e.g., climate, associated with the geographic space defined by those records (Pearson and Dawson 2003; Guisan and Thuiller 2005). This modeling approach assumes that species are in at least quasi-equilibrium with their environment (Guisan and Thuiller 2005; Wiens and others 2009) and that the species-climate relationships currently inherent in the species' distribution will hold true in the future (Varela and others 2009). The basic requirement for correlative modeling is presence data or abundance records for the target species, though combined presence/absence data potentially improves predictive accuracy by reducing overprediction error (Guisan and Thuiller 2005; Pearson and others 2006). Table 2 in Guisan and Thuiller (2005) lists important considerations in developing an SDM.

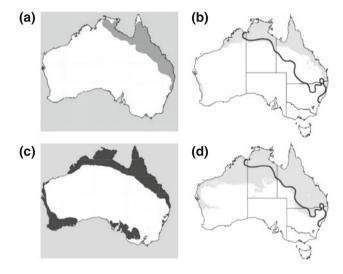
As a method for forecasting distributional changes in species, some consider mechanistic models more robust than correlative models and more likely to capture noanalog future climate conditions (Pearson and Dawson 2003; Kearney and Porter 2009; Rodder and others 2009). This is, in part, due to their respective representations of fundamental and realized niche. In addition, the correlative approach defies the limits of statistical inference by extrapolating relationships between species distribution and environmental variables into un-sampled geographic space to map potential changes in species' distributions. Forecasts based on mechanistic models require no such extrapolation (Kearney and others 2008; Monahan 2009). However, extensive application of mechanistic SDMs for species vulnerability assessment is difficult because the models require detailed data and computational resources (Kearney and Porter 2009). The physiological tolerances of most species to climatic conditions are not well known and are sometimes subject to intra-specific variation within a geographic range (Pearson and Dawson 2003). Moreover, the output of mechanistic models does not consider the indirect effects of climate-induced changes in disturbances that impact habitats and biotic interactions; thus they reflect nearly all possible but not necessarily probable areas of a species' future range. Mechanistic and correlative models can generate very different projections, making it necessary to fully understand underlying assumptions of the modeling methods and the appropriate applications of the respective outputs (Text Box 1). See Table 1 in Kearney and Porter (2009) for a comprehensive comparison of mechanistic and correlative approaches to species distribution modeling, including advantages and disadvantages.

Assessing Relative Vulnerability with Evaluative Frameworks

In response to limits on time, data availability and computational capacity for modeling, conservation organizations and management agencies have begun designing evaluative frameworks-question-based non-spatial assessments that provide a relative index of vulnerability of target organisms to climate change. Like the species distribution models, the vulnerability indices combine information about species sensitivity to and exposure to anticipated changes in conditions directly and indirectly related to climate change. While this type of assessment is a fairly recent addition to the complement of climate change adaptation planning tools, examples of their application by organizations and agencies exist (e.g., Glick and Stein 2011). We discuss three frameworks here: NatureServe's Climate Change Vulnerability Index (CCVI-Young and others 2009); a vulnerability index developed by the Rocky Mountain Research Station (USFS-RMRS) of the United States Forest Service (Finch and others 2011) to assess vertebrates; and a framework developed for the Environmental Protection Agency's National Center for Environmental Assessment (EPA-NCEA) to evaluate threatened and endangered species (US Environmental Protection Agency (US EPA) 2009). The frameworks of the index tools are spreadsheet or tabular based, and each addresses a set of factors relevant to the climate response of a species through a systematic process. While the tools analyze many common sensitivity and exposure factors, their structures, some content, and the guidelines to their respective scoring systems differ (Table 2).

The NatureServe CCVI is programmed in Microsoft© Excel and is designed to incorporate data generated using GIS analyses of species' distributions and future climate projections; however, a more qualitative assessment may be conducted. The CCVI has three principal components, which include: (1) climate exposure based on future Text Box 1 Comparing correlative and mechanistic models. a Current distribution of cane toad (Chaunus [Bufo] marimus) documented in Australia; b the potential distribution using bioclimatic envelope model with climate data from native range in South and Central America-from Kearney and others 2008 based on Sutherst and others 1995: **c** the potential distribution using a bioclimatic envelope model with climate data from Australian distribution-from Urban and others 2007; and **d** the potential distribution projected using a mechanistic model-from Kearney and others 2008. Note: Maps (a) and (c) courtesy of Urban and others 2007, Figure 1, p. 1414, Royal Society Publishing. Maps (**b**) and (**d**) courtesy of Kearney and others 2008, Figure 1, p. 424, John Wiley and Sons Publishing

The cane toad (Chaunus [Bufo] marimus), a native of South and Central America, was introduced to northeastern Australia in 1935. Due to its rapid and extensive spread both along the coast and into the arid interior and the resultant decline of native amphibian species, the cane toad is considered invasive, prompting research into the potential suitable habitat for the species and capacity for additional deleterious impact. The distribution maps (a-d) below illustrate the differences in predictions of potential geographic range generated by bioclimatic models (Sutherst et al. 1995, Urban et al. 2007) and a mechanistic SDM (Kearney et al. 2008), all based on current climatic conditions. The methodological comparisons also demonstrate the influence of the predictor variable selection and source-climate data sets on results. The shaded area in panel (a) and the thick black lines in panels (b) and (d) represent the currently documented range of cane toad in Australia for reference; map (a) shows only the dense core of existing populations, whereas the line in (b) and (d) captures the expanding edge. One of the first bioclimatic modeling efforts to predict the expansion capacity of the cane toad in Australia used climate data (rainfall, humidity, temperature) from the native range of cane toad in South and Central America (Sutherst et al. 1995), Shown in map (b), the results do not even capture the currently documented range of the species in Australia. Map (c) displays the results of a bioclimatic model with the same variables as Sutherst et al. (1995) but using the climate data associated with the current distribution of cane toad in Australia (Urban et al. 2007). The model underlying map (c) also incorporates the influence of anthropogenic disturbance (e.g., road cover, land use), to which cane toad is know to respond positively and suggests an expanded area of suitable habitat and much enhanced potential for range expansion. The mechanistic model of Kearney et al. (2008) explicitly considers the differing energy and water-balance constraints on the egg, larval and adult stages of the cane toad life cycle (d). Interestingly, the mechanistic model prediction excludes the southernmost areas identified by Urban et al. (2007), while expanding the potential for the cane toad's spread to the interior of Australia (d). This difference may be caused by the important role that anthropogenic disturbance plays in controlling the spread of cane toad, which is not included in the Kearney et al. (2008) model. If so, this underscores the importance of land use considerations in climate response forecasts.



projections of temperature and water balance for the assessment area; (2) indirect climate exposure to factors such as sea level rise and changes in land use through the expansion of biofuels or other types of climate mitigation; and (3) information addressing typical sensitivity factors (e.g. dispersal, physiological tolerance, biotic interactions, genetics) (Young and others 2009). Responses are required in the three main sections in order for a score to be calculated. The user may make multiple selections in response to the factors in tool components (2) and (3), if there is minimal information about the influence of a factor on the species' vulnerability. The magnitude of exposure is used to weight sensitivity responses in a way that minimizes vulnerability, regardless of exposure, if a species shows no inherent sensitivities. A fourth, optional, section incorporates observed or modeled species' responses to climate change into the index score, if this information is available. Except for climate exposure inputs, the factor responses are selected from an ordinal scale that reflects the potential influence of the factor on overall vulnerability. Once the required inputs have been made to the spreadsheet, an underlying algorithm automatically generates a categorical vulnerability score or rank for multiple species, descriptive of expected response to climate change. Specific guidelines for responding to the factor questions are located on tabs in the workbook. In another workbook tab, responses for completed species assessments are saved in a preformatted table, in which the contributions of the factors toward increasing or diminishing vulnerability are highlighted. The NatureServe CCVI does not consider non-climate stressors in its evaluation of vulnerability, as it is designed to be complementary to an existing product, the

Table 2Factors addressed inthe NatureServe, USFS-RMRSand EPA climate vulnerabilityindices (Young and others 2009,Finch and others 2011; US EPA2009)

	NatureServe*	USFS-RMRS	EPA-NCEA
Sensitivity			
Physiology-based climatic thresholds	~	~	~
Dispersal	~	~	~
Habitat specialization	~	~	~
Biotic interaction/dependence	~	~	~
Seasonal migrations/movements	~	~	
Phenology	~	~	~
Other (e.g., genetic diversity, plasticity)	~	~	
Exposure			
Temperature/precipitation change	~	~	~
Habitat loss/gain current range		~	~
Habitat available in projected range			~
Increase extreme weather		~	~
Barriers to dispersal (land use/topographic)	~	(V)	(🖌)
Non-climatic stressors (e.g., land use, pollution)	~		~
Climate and other information			
Climate projections	~	~	~
Vegetation change projections		 ✓ 	~
Modeled species' response	~		~

version due April 2010. (🗸) Mod Indirectly considered

*Currently under revision. New

NatureServe Conservation Status assessment (http://www. natureserve.org/explorer/).

The four sections of the USFS-RMRS vulnerability assessment tool incorporate the elements of sensitivity and exposure implicitly through questions addressing species' traits related to habitat, physiology, phenology and biotic interactions (Finch and others 2011). Like the NatureServe CCVI, the USFS-RMRS tool is designed to assess species within a predefined geographic area. Future climate projections for the assessment area are required, and information about other climate-related impacts offers additional nuance to responses. Vegetation model output for the assessment area is important for responding to the habitat questions. Ordinal scores, which include positive and negative values depending upon their influence on vulnerability, are assigned to each question in reference to brief guidelines embedded in the spreadsheet. The assessor gauges the uncertainty of the responses to each section's questions, based on the availability of information, using categorical values (i.e., 0, 1, 2). Results are considered relatively certain if information is available for the given species to answer all or most of the questions. Results become increasingly uncertain if the assessor is relying on information from similar species or broad generalizations to answer the questions. The uncertainty estimates assigned to the four sections of the tool are qualitative; do not reflect the uncertainty related to the projections of future climate and vegetation used in the analysis; and are currently not incorporated into the final vulnerability scores of the species. A more detailed description of the overall scoring system is outlined in a separate guidance document available from the USFS. As each species is evaluated, the spreadsheet calculates an overall total, and presents subtotals with reference to the four sections of the tool in a table to help identify key sources of vulnerability. Once all species are evaluated, comparisons between the overall scores determine their relative vulnerability within the assessment unit.

The EPA tool differs from the other two assessment tools in that it was explicitly developed to evaluate the relative vulnerability of species identified as threatened and endangered under the U.S. Endangered Species Act to determine how their conservation status might be altered by climate change (U.S. Environmental Protection Agency (US EPA) 2009). The first two parts of this framework assess the relative vulnerability of each species to existing stressors and to climate change separately. The existing stressor section includes variables related to population size and trends, while the climate section targets sensitivity factors to evaluate the potential for increased risk of extinction. Scoring guidelines for both sections are presented in a document summarizing the method and a case study (US EPA 2009). A matrix then integrates the responses to factors underlying the two types of vulnerability into an overall vulnerability score for the assessed species. As in the NatureServe tool, multiple responses to factor questions are allowed and used to evaluate the overall uncertainty in vulnerability result.

The information required for characterizing a species' exposure to different climatic factors in all three vulnerability frameworks is generally obtainable from published climate and/or vegetation forecasts and web-based tools (e.g., Climate Wizard-Girvetz and others 2009, Santa Clara University, Bias Corrected and Downscaled WCRP CMIP3 Climate Projections Santa Clara University, Bias Corrected and Downscaled WCRP CMIP3 Climate Projections. Accessed 14 Jan 2010). To address the sensitivity factors of species, the user leverages empirically derived, published literature about species' tolerances, life history traits and ecology. If available, the published results of SDM-based predictions represent another source of species vulnerability information. However, beginning with knowledge of species natural history (i.e., the input of experts) ensures a more rapid assessment (Young and others 2009), and is the basis for the EPA-NCEA approach (US EPA 2009). The informational detail and questionbased processes that inform vulnerability indices provide not only the relative likelihood of species impact; they also indicate through what means those impacts might occur, as highlighted in both the USFS-RMRS and NatureServe output tables. Pinpointing the source of vulnerability allows managers to identify plausible mechanisms and to possibly anticipate potential non-linear responses.

While the results of index-based assessments are not inherently spatial, much of the information incorporated is GIS-based, including the projections of climate and vegetation change, land use data and other aspects of exposure. Due to the accessibility of geospatial environmental information, the results of vulnerability indices can be mapped to examine the spatial patterns of climate change vulnerability. For example, Davison and others (Davison J: personal communication, May 2010) analyzed the spatial patterns of vulnerability derived from an application of the USFS RMRS assessment tool to species of interest in the Coronado National Forest in southwestern U.S. in relation to land use and environmental variables. Using a different approach to risk assessment, Williams and others (2009) identified specific locations within the range of western cutthroat trout populations that would be most exposed to certain conditions driven by climate (e.g., high summer water temperatures, flooding and wildfire). Population persistence was initially assessed using an index of conservation status, the results of which were interfaced with a map of concentrated exposure. Similar approaches have been used to identify the spatial patterns of climate exposure in moisture-sensitive vegetation types (e.g., Enquist and Gori 2008).

Addressing the Limitations and Uncertainties of Assessment Approaches

Prospective sources of uncertainty in the impact assessment approaches for developing strategies for climate change adaptation are numerous (e.g., Beaumont and others 2008; Lawler and others 2010a). Impact assessments represent the foundation of the planning process, and the tools currently available can help to identify potential vulnerabilities. However, the uncertainties and limitations inherent in the various methods need to be acknowledged and deliberately taken into account in the application of assessment results, through scenario-based planning, adaptive management and/or other approaches in follow-up planning and implementation efforts (e.g., Lawler and others 2010a; Pearson and others 2006; Marmion and others 2009; Buisson and others 2010).

Climate Models

While some sources of uncertainty span the methods of vulnerability assessment and others are method-specific, layering of uncertainty is inherent to all approaches to varying degrees. The most universal source of uncertainty in assessing species vulnerability to future climate change is associated with the outputs of global climate models, also called general circulation models (GCMs). The elements of GCMs that confer uncertainty are their spatial resolution (the finest-scale grids of which are approximately 80 km (50 miles) on a side), variation in model algorithms and parameterization, and scenarios of future greenhouse gas emissions that underly projections (see Text box 2). Another factor contributing to uncertainty in climate model output, particularly in remote and mountainous regions, is the paucity of instrumentation recording recent climate (Beale and others 2008; Rodenhuis and others 2009). Because climate instrumentation density is greater in valleys, uncertainty associated with this uneven distribution is conferred to climate data products (e.g., Daly and others 2008) used in projections and other applications. Additionally, the change in climate averages and trends calculated from model forecasts may vary as a result of the baseline period chosen for comparison (e.g., 1961-1990 versus 1971-2000), due to decadal-scale climate variability (Swetnam and Betancourt 1998). Moreover, averaged differences leave out the temporal variability and extreme events, to which species are sometimes most responsive, and they miss the many effects of topographic variation and land cover important at the local scale (Parmesan and others 2000; Gray and others 2006; Wiens and Bachelet 2010).

Species Distribution Models

While species distribution models have the potential to provide important insights and to aid decision-making regarding species response to climate change, biological and model-based sources of uncertainty add to the uncertainties associated with climate projections. Beaumont and others (2008) provide a thorough review of climate model Text Box 2 More about climate models

Models used for future climate projections are representations of the complex dynamics of the climate system, including patterns of atmospheric circulation and oceanic processes. Within the models, the processes that control climate are expressed as mathematical equations derived from scientific laws and empirical data. Because future concentrations of greenhouse gases in the atmosphere are uncertain, emission scenarios are employed in the climate projections. Emission scenarios are approximations of future conditions based on assumptions about technological changes, and social, economic and policy developments and incorporate feedback mechanisms that lead to the crossing of critical thresholds.

The algorithms and parameters that drive the several models commonly used often generate different projections of future temperature and precipitation. This variability occurs even when a common emission scenario drive model output, compounding the uncertainty derived from two sources. To validate models that estimate future changes in precipitation and temperature, model outputs hindcasting the last century are compared to the actual climate patterns observed during that time. Assessments like this help identify which components of the climate system are best captured by which models. Typically, different models capture different elements of a climate more precisely than others, especially at the regional scale, due to the effects of processes operating at spatio-temporal scales smaller than the coarse resolution of most climate models. Global climate projections for temperature, particularly during the early part of the 21st century, are considered relatively robust by the scientific community because temperature fluctuations occur across large areas represented by multiple grid cells. Also, within this period the differing emission scenarios result in consistent projections (Solomon et al. 2007). The climate models typically project a common direction of change, while the magnitude varies. Precipitation projections are less certain because precipitation events typically affect areas smaller than that of the grid cells used in models, particularly in mountainous areas where elevation and topography play important roles in precipitation patterns. Thus, precipitation output for given region can vary between models, sometimes widely, in both magnitude and direction of change. Yet given the consistency with the observed response of precipitation to warming temperatures through the 20th century, the patterns projected for precipitation at the global scale are also considered robust, particularly shifts in seasonality.

Climate change projections are most reliable at the global scale; however, regional climate models are under development that more accurately capture the environment heterogeneity, local atmospheric circulation, and seasonal climate patterns (e.g., rainfall) key to informing management typically enacted at finer spatio-temporal scales. Downscaling techniques are currently used to integrate global climate model output into regional climate projections. GCM output is downscaled either by using statistical equations that relate variations in global climate to local climate (i.e., statistical downscaling) or by using meteorological models that integrate knowledge of the effects of global patterns on local weather conditions (i.e., dynamical downscaling). While these techniques provide finer-resolution output, results from the current methods for downscaling are less reliable in areas of complex topography (Wiens and Bachelet 2010). Additionally, downscaling in general tends to compound the uncertainty of the GCMs because patterns are interpolated or extrapolated to provide finer resolutions (Wiens and Bachelet 2010).

General source: Southwest Climate Change Network (SWCCN) http://www.southwestclimatechange.org/climate

uncertainties (and other relevant uncertainties) in the context of species distribution models.

As with climate models, several model-based factors contribute to uncertainty in SDMs. The different statistical techniques underlying species distribution models yield differences in response results, even when driven by the same climate projections (Lawler and others 2006; Pearson and others 2006), and no one technique has been shown to be most accurate. Forecasts of species distributions also depend on the selection of predictor variables (Beaumont and others 2008) and decision thresholds (Pearson and others 2006), and the assumptions made by algorithms in correlative models to extrapolate relationships into the future (Pearson and others 2006).

In addition, there is ambiguity about how much of a species' fundamental niche is captured in correlative models that reflect realized niche (Pearson and Dawson 2003; Guisan and Thuiller 2005). While analyses whose spatial extents capture the complete environmental range of a species more accurately represent the full, realized niche (Thuiller and others 2005), there is also ample evidence for variability in species-climate relationships within ranges that potentially complicate responses (Beale and others 2008; Monahan 2009; Lavergne and others 2010). Moreover, the bioclimatic interactions and interacting effects of other anthropogenic stressors that influence current range are only captured implicitly in correlative models and may not remain stable through time or space (e.g., Suttle and others 2007; Pearman and others 2008; Varela and others 2009; Lavergne and others 2010). Invasive species biogeography provides modern examples, such as fire ants introduced to North America that have occupied areas with climate outside the envelope of the species' native range in South America (Fitzpatrick and others 2007).

Consequently, modeled forecasts may overlook areas with suitable conditions, due to unknown potential interactions or physiological tolerances. Additionally, understanding temporal details of a species' niche is important for organisms for which the environmental requirements for regeneration may differ from those for maintenance of mature populations (Jackson and others 2009a).

The spatial and temporal scale of species and environmental data used in models also introduces uncertainty, because species' distributions and the dominant environmental controls over such distributions operate on multiple interacting spatial extents and resolutions (Pearson and Dawson 2003). Uncertainty can arise from mismatches between the scale of data describing species and that describing environmental information, and between the scale of environmental heterogeneity in the region of interest and the resolution of available data (Thuiller and others 2005; Kearney and Porter 2009; Illan and others 2010; Wiens and Bachelet 2010). Similarly, uncertainty is increased if the resolution and/or extent of available data are inappropriate to address the modeling objectives (Pearson and Dawson 2003; Beaumont and others 2008). With regard to species occurrence data, if the spatial resolution is coarse, especially in the case of sessile organisms, errors of commission may result in overestimation of suitable habitat for species (Guisan and Thuiller 2005; Monahan 2009). Errors of omission can occur if the temporal resolution or extent of presence data precludes precise or relevant documentation of species (Monahan 2009). Finally, there is some evidence that only a subset of the climate space that could be utilized by a species currently exists, thereby limiting the parameterization and future forecasts of current SDMs (Jackson and Overpeck 2000).

Other Sources of Uncertainty

The limited availability of and variability in data describing species occurrence, physiological tolerances and other factors that constrain species' ranges restricts many of the impact assessment approaches reviewed here (e.g., Lawler and others 2009). Methods have been developed to address some data limitation issues, for example, species with limited occurrence records (Pearson and others 2007). Additionally, the ecological niche properties associated with generalist versus specialist species may result in unexpected patterns of sensitivity to climate. For example, Merrill and others (2008) found that warming temperatures along an elevational gradient drove an upward shift of the lower range margin of a specialist butterfly. However, the species' expansion into climatically suitable areas at upper elevations was apparently forestalled by the distribution limit of the butterfly's larval host plant. Moreover, while a broad climatic niche generally relates to greater tolerance to change, the vulnerability of species with marginal or restricted ranges depends in large part on the geographic location of their occurrence relative to climatic gradients (Thuiller and others 2005; Beale and others 2008). Finally, non-plant species often respond most directly to changes in their habitats, specifically vegetation structure and composition, and this can be a confounding factor in deducing relationships with climate (Lavergne and others 2010). Projections of future vegetation distribution, which are driven by climate projections, may be used to address potential habitat change in vulnerability assessments.

Because they do not incorporate climate projections, the primary limitation of empirical observations is that they have modest predictive value beyond the near future and are rarely transferable beyond the study extent (Lawler and others 2010a, b). While results inform potential trends, they are not readily extrapolated; no-analog communities have arisen from unique species assemblages in the past and will likely again in response to the no-analog climates and the rate of change projected for the coming century (Williams and others 2007; Colwell and Rangel 2009).

An important drawback of vulnerability indices arises from the fact that they are applied within management boundaries rather than species distribution limits and do not explicitly consider the impact to the species in the context of their broader distribution. The relative nature of the results limits their application outside the region of interest. Additionally, because their output is not spatial, vulnerability indices themselves do not directly address where within its management unit a species might be most vulnerable to climate change.

Dealing with Uncertainties and Limitations

Uncertainties associated with each stage of the assessment process should be acknowledged, quantified if possible, and reduced or embraced as much as feasible relative to the goal of the vulnerability assessment. Limitations on the application of the assessment itself should be clearly expressed. While many authors endorse the addition of this information when reporting results, it is too often overlooked when results are applied in a management context (e.g., Buisson and others 2010).

Means for appraising the magnitude of uncertainty associated with predictions of species' responses are becoming increasingly common. All of the vulnerability indices we examined included some estimate of the uncertainty associated with each species' output, based upon the confidence in the species' information used to determine how the multiple sensitivity and exposure factors influence vulnerability. In the NatureServe tool, users may select more than one answer to capture response ranges if information about the species' sensitivity to a factor is limited or unavailable. The tool generates a confidence level for each species by incorporating any multiple responses to the vulnerability factors into Monte Carlo simulations that recalculate CCVI the score. Confidence in the initial results is assigned using the distribution of the simulated scores (Young and others 2009). In the EPA-NCEA framework, uncertainty is captured in two ways, in the multiple responses allowed for each factor and through a confidence level (i.e., high-medium-low) assigned by the user to each factor response (US EPA 2009). In the USFS RMRS tool, only one response is permitted to each factorrelated question, and an evaluation of uncertainty is assigned by the user to the four sections of the framework based on the availability of information used for scoring within each (Finch and others 2011).

To acknowledge and reduce uncertainty with regard to climate models, Beaumont and others (2008) advise the following steps, all of which are relevant to any assessment approach that incorporates climate projections. These recommendations include: (1) provide information about the climate models, emission scenarios and downscaling technique used in projections; (2) select climate model output based on how well model(s) simulate the components of climate relevant to the questions and region of study; (3) choose model output based on the extreme of current emission scenario options, given that recent actual increases exceed the most dire scenarios used in Fourth IPCC report (Solomon and others 2007); (4) understand and report model ensemble averages, whether they are multiple realizations of a single model or a combination of multiple models; (5) if climate model output is poor or not relevant to the study region, use idealized climate scenarios based on observed historical climate trends or relevant paleoclimatological reconstructions (Beaumont and others 2008). Recommendations 2, 4 and 5 should also be considered when using SDMs in vulnerability assessments (Pearson and others 2006).

Even though species distribution modeling may seem beset by uncertainty, SDMs remain important as a method for approximating impacts of climate on species' ranges, especially in combination with other approaches (Lawler and others 2010b). A fundamental step toward reducing uncertainty is to evaluate the precision and predictive performance of individual bioclimatic modeling techniques through statistical comparisons between the observed and modeled modern distributions of species (e.g., Pearson and others 2006). Such comparisons can highlight consistencies between predictions and can be used to generate probability distributions of species responses (Lawler and others 2006; Pearson and others 2006; Beaumont and others 2008; Wiens and Bachelet 2010). However, it is important to note that consensus between models under current conditions does not always lead to agreement in forecasts of future distributions (e.g., Bachelet and others 2003). Comparing the results of mechanistic models and bioclimatic models allows for identification discrepancies between the responses in fundamental and realized niches to provide insight into the uncertainty in species' response (Thuiller and others 2005; Kearney and Porter 2009). Qualitative comparisons with the direction and magnitude of past responses can also help inform accuracy of projected changes, although, again, past patterns may have limited relevance for future response (Martinez-Meyer and others 2004; Pearson and others 2006; Lawler and others 2009).

In recent years, various additional measures have been investigated for reducing uncertainty in bioclimatic models. Comparable to ensemble models in climate projections, consensus methods of bioclimatic modeling offer one means to minimize the probability of errors and thus the variability in projections of range changes (e.g., Marmion and others 2009; Buisson and others 2010). Predictions based on ensemble forecasts of species distributions are created from combining the best-performing single algorithms into a consensus model; however, caution in the application of output is warranted. While reducing variability, consensus methods using ensembles do not necessarily offer greater precision and continue to represent hypotheses of the magnitude and direction of change in species distributions. Sensitivity analyses are another means by which to examine differences between results arising from the variability in model algorithms and inputs (e.g., Beaumont and others 2008). Incorporating other factors and processes that affect species distributions is another measure to address uncertainties. Examples include the use of hierarchical frameworks to capture cross-scale temporal and spatial interactions of controls over distribution (Guisan and Thuiller 2005; Luoto and others 2007), the coupling of bioclimatic and dispersal/population models to incorporate migration capability (Keith and others 2008; Anderson and others 2009; Lawler and others 2010a, b; Lavergne and others 2010), and the inclusion of species and their host plants (Araujo and Luoto 2007) or species assemblages (Baselga and Araujo 2009) to model biotic interactions. In general, new modeling approaches continue to be evaluated and refined to identify and lessen uncertainty in species vulnerability and impact assessments (e.g., Buisson and others 2010).

Incorporating Vulnerability Assessments into the Adaptation Planning Process

Impact assessments are often considered a critical first step toward engaging in the process of climate adaptation planning and implementation. The results of assessments help to prioritize targets and define feasible management

goals, to identify management actions based on the factors underlying species' vulnerability, and allocate limited resources for follow up planning efforts (e.g., Glick and Stein 2011; Jackson and others 2009b; Text box 3. The climate change effects forecast in some manner by all of these approaches are only hypotheses of biological response. However, with awareness of the uncertainties and caveats across and among vulnerability assessments, the selection of an approach or multiple approaches and informed application of results can begin to guide climate change adaptation planning. For resource managers, the overall objective of assessments and the subsequent planning process is to develop an understanding of whether and how climate change effects may inhibit the fulfillment of existing management goals and, therefore, what actions to take (West and others 2009).

Considering Spatial Scale, Biological Scope, and Resources

With this in mind, there are several factors to consider when choosing among assessment methods. From the start, both geographic and biological scope of the impact assessment should be clearly defined and based on a specific objective or outcome (Fig. 2). Within the management unit or region of interest, should all species be evaluated, or just threatened and endangered species or other designated species of concern, such as priorities identified in State Wildlife Action Plans? Particular plant communities or species functional types represent other options for defining the biological scope. Also relevant to scope, species may be more or less suited to a particular vulnerability assessment tool. For example, it may be more appropriate to use vulnerability indices than bioclimatic modeling for specialist species with known dependencies on host plants or other biotic interactions, or, perhaps, model both species in an important relationship (e.g., Merrill and others 2008). Hierarchical assessments represent a comprehensive strategy, whereby sets of organisms are evaluated with different methods, potentially through a step-wise process, based on the level of concern and on the availability of resources or necessary data sets (e.g., Case and Lawler 2011). While a multi-approach process may provide a thorough assessment, the investment of time and resources could be significant.

At the same time, the spatial extent of the management unit or region of interest limits the suitability of assessment methods. For example, in correlative bioclimatic models accuracy is improved if environmental data representing the entire species range is included (Thuiller and others 2004). A related consideration is the availability of data at a resolution that represents the dominant influences controlling species' distribution patterns (Pearson and Dawson 2003; Guisan and Thuiller 2005). Thuiller and others

Text Box 3 Scenario planning and adaptive management

Scenario-based management planning is a means to explicitly address the uncontrollable and irreducible uncertainty inherent in climate change projections and impact assessments based on the response of biological and physical ecosystem components (Peterson et al. 2003, Solomon et al. 2007, Moss et al. 2010). In brief, scenario planning, in the context of climate change, harnesses uncertainty by exploring the potential consequences of adaptation strategies and actions for a range (or the most likely set) of plausible climate change futures (Peterson et al. 2003, Baron et al. 2009, West et al. 2009). The optimal actions are those that are robust under that range of future conditions. Even with the potential benefits of scenario planning, the process requires a means to deal with the uncertainties in the outcomes of management decisions and actions based on the hypotheses of change generated by climate impact assessments. Adaptive management is an approach to decision-making and action-implementation long-embraced by resourcemanagement institutions. The iterative framework of adaptive management includes experimental implementation, monitoring, and management refinements as additional information becomes available or unexpected outcomes occur (e.g., Holling 1978, Millar et al. 2007, Lawler et al. 2010a). Scenario planning for developing climate adaptation strategies can be readily integrated into this established management process (Jackson et al. 2009b, West et al. 2009, Neely et al. 2010).

Another element of the adaptation challenge is the socio-economic context underlying resource management decisions (Lawler et al. 2010a, Moss et al. 2010). While detailed discussion is beyond the scope of this paper, this important topic merits brief mention. Most decisions are made and implemented in landscapes that exhibit varying degrees of human modification inside and outside a management unit, and where impacts on ecosystems do not adhere to ownership boundaries (Theobold 2004, Lawler et al. 2010a). Thus, such decisions necessarily involve multiple stakeholders and require collaboration. Notably, the social networks tied to these landscapes have the capacity to facilitate or inhibit the adaptation process (Hahn et al. 2008). The scenario approach to planning offers an opportunity to build understanding and strengthen social networks among sometimes-disparate interests through the discussion and analysis of multiple possible outcomes of decisions (e.g., Peterson et al. 2003, Moss et al. 2010).

Examples of management organizations dealing with climate-related uncertainty in management decisions are described in Lawler et al. (2010a) and Hansen et al. (2010).

(2005) recommend that the resolution of the data used in bioclimatic analyses be comparable to the environmental heterogeneity of the assessment region; however, such data are rarely available for complex landscapes like mountain areas (Wiens and Bachelet 2010). Index tools offer an alternative in landscapes where fine-grained processes and patterns are important, such as those related to complex topography and even the gradient of land use experienced by a species (Theobold 2004; Luoto and others 2007). NatureServe recommends application of its vulnerability index to spatial scales from a management unit (such as an individual protected area) to a multi-state region and addresses barriers to dispersal, both in the form of natural topographic features and land uses representing unsuitable habitat (e.g., Wildland-Urban Interface Maps 2010; Young and others 2009). The USFS-RMRS tool is applicable in similar sized management units or even across a species' range (Finch and others 2011).

Temporal factors such as the decision-making and management horizons should also guide the choice of assessment approach. If rapid decisions (<1 year) are required because immediate management actions are anticipated, vulnerability index tools may be appropriate, particularly if conducted by individuals with speciesspecific expertise (Young and others 2009). Because species' sensitivity factors and information related to exposure are noted through the evaluation process, vulnerability indices could potentially save time by reducing the steps between assessing the potential impact and identifying management. Determining the characteristics that increase or reduce vulnerability at the outset may also serve to group species with linked vulnerabilities through shared dependence on an ecosystem feature, such as habitat type (e.g., Davison, J: personal communication, May 2010). Species distribution models, especially mechanistic models, are information-intensive, requiring proficiency in the compilation of spatial datasets and model development. SDM-type approaches may be more appropriate for understanding the broad impacts of climate change at subcontinental and greater spatial scales and at multi-decadal or longer time steps (Fig. 2; Lawler and others 2010b). In contrast, vulnerability indices outline a process through which managers, especially those who have not yet explicitly incorporated climate change into their management strategies, can take at least a preliminary step toward understanding the vulnerability of species of concern to climate change. This step may occur while improved understanding about how climate may change within their management units is developed through evolving efforts toward increasing the certainty in climate projections, biological response and physical process models. Embracing the variability in climate projections by employing plausible future scenarios in vulnerability assessments and planning exercises to gauge differences in impacts and potential management responses is another valuable means for dealing with uncertainty (Jackson and others 2009b; Text Box 3).

Integrating assessment tools may also lead to enhanced understanding of the mechanisms underlying species' vulnerability, further aiding the identification of appropriate management actions. The vulnerability indices we examined explicitly incorporate modeled projections as part of the evaluation (Young and others 2009; Finch and others 2011). Additionally, forecasts from species distribution models might be used to identify patterns of vulnerability within a species range. A finer-scaled assessment using an index tool could then quantify this vulnerability relative to other organisms in the management unit. Alternatively, as modeling tools are recognized complements to expert assessments of vulnerability (Thuiller and others 2005), index-based identification of sensitivities common to a group of species might lead to a follow-up modeling effort targeted on that common component, such as a habitat type or a key element in a set of trophic interactions (e.g., shared prey species; Case and Lawler 2011). However, expert opinion may indeed provide valid assessments that are equal to and less time-consuming than index or modeling tools. Knowledge of species' sensitivities alone is an indication of potential vulnerability (West and others 2009) and, given time or resource constraints, may be the only avenue for assessing organisms that exhibit fine-tuned climate sensitivities (e.g., seasonal precipitation) linked to variables not represented in current climate projections (Beale and others 2008).

Conclusions

Because climate change is underway, impact assessment and adaptation planning cannot be put on hold while science and management are refining our understanding of future climate conditions and biological responses. With readily obtainable geospatial environmental information, continual refinements in climate projections, and tools to integrate them available on-line, the capacity to undertake species vulnerability assessments is accessible to many engaged in resource management. Each of the assessment approaches we reviewed-the documentation of past changes, forecasts of mechanistic and correlative bioclimatic models and vulnerability indices-has limitations related to data and resource requirements and to application, as well as the sources of uncertainty that constrain its suitability for different applications. However, thorough consideration of the objectives, scope, scale, time frame and available resources for a climate impact assessment allows for the selection of an appropriate approach to develop initial hypotheses about species' vulnerabilities. These preliminary assessment results and an informed awareness of their limitations contribute important information to the adaptation planning process, that is, undertaking the next steps of identifying the management strategies and targeted actions that will likely become necessary to sustain functioning ecosystems and their associated services into the centuries to come.

It is important to remember that, even after linking the results of impact assessments to adaptation planning outcomes, other hurdles remain for the implementation of climate-informed actions in natural resource management. There are barriers posed by the legal and policy framework of environmental regulation, which currently fosters the preservation and restoration of ecological systems to twentieth reference conditions, many of which are likely no longer supported by rapidly changing climate (Craig 2010). More significantly, there is limited public acknowledgement of the ecological and socio-economic issues related to climate change, and thus, minimal public understanding and acceptance of adaptation efforts and the devotion of resources toward them. Federal-level acknowledgement of the need for climate adaptation strategies, starting with vulnerability assessments (e.g., U.S. Fish and Wildlife Service (USFWS) 2010; Salazar 2009), requires further action to address the constraints on implementation imposed by current regulations, as well as by public support.

Acknowledgments This research was supported in part by funds provided by the Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture. We appreciate the thoughtful comments of three anonymous reviewers and M. Cross that contributed greatly to the manuscript.

References

- Anderson BJ, Akcakaya HR, Araujo MB, Fordham DA, Martinez-Meyer E, Thuiller W, Brook BW (2009) Dynamics of range margins for metapopulations under climate change. Proceedings of the Royal Society B-Biological Sciences 276:1415–1420
- Araujo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16:743–753
- Bachelet D, Neilson RP, Hickler T, Drapek RJ, Lenihan JM, Sykes MT, Smith B, Stich S, Thonicke K (2003) Simulating past and future dynamics of natural ecosystems in the United States. Global Biogeochemical Cycles 17:1045
- Baron JS, Gunderson L, Allen CD, Fleishman E, McKenzie D, Meyerson LA, Oropeza J, Stephenson N (2009) Options for national parks and reserves for adapting to climate change. Environmental Management 44:1033–1042
- Baselga A, Araujo MB (2009) Individualistic vs community modelling of species distributions under climate change. Ecography 32:55–65
- Beale CM, Lennon JJ, Gimona A (2008) Opening the climate envelope reveals no macroscale associations with climate in

European birds. Proceedings of the National Academy of Sciences of the United States of America 105:14908–14912

- Beaumont LJ, Hughes L, Pitman AJ (2008) Why is the choice of future climate scenarios for species distribution modelling important? Ecology Letters 11:1135–1146
- Beever EA, Brussard PE, Berger J (2003) Patterns of apparent extirpation among isolated populations of pikas (Ochotona princeps) in the Great Basin. Journal of Mammalogy 84:37–54
- Buisson L, Thuiller W, Casajus N, Lek S, Grenouillet G (2010) Uncertainty in ensemble forecasting of species distribution. Global Change Biology 16:1145–1157
- Case M, Lawler JJ (2011) Case study 7. Pacific Northwest climate change vulnerability assessment. In: Glick P, Stein BA (eds) Scanning the conservation horizon: a guide to climate change vulnerability assessment. National Wildlife Federation, Washington, pp 129–136
- Chen IC, Shu HJ, Benedick S, Halloway JD, Chey VK, Barlow HS, Hill JK, Thomas CD (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. PNAS 106:1479–1483
- Colwell RK, Rangel TF (2009) Hutchinson's duality: the once and future niche. Proceedings of the National Academy of Sciences of the United States of America 106:19651–19658
- Craig RK (2010) "Stationarity is dead"—long live transformation: five principles for climate change adaptation law. Harvard Environmental Law Review 34:9–74
- Daly C, Halbleib M, Smith JI, Gibson WP, Doggett MK, Taylor GH, Curtis J, Pasteris PP (2008) Physiographically-sensitive mapping of temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064
- Enquist C, Gori D (2008) A Climate change vulnerability assessment for biodiversity in New Mexico, part I: implications of recent climate change on conservation of priorities in New Mexico. The Nature Conservancy in New Mexico, 69 pp
- Finch DM, Friggens M, Bagne KE (2011) Case study 3. Species vulnerability assessment for the Middle Rio Grande, New Mexico. In: Glick P, Stein BA (eds) Scanning the conservation horizon: a guide to climate change vulnerability assessment. National Wildlife Federation, Washington, pp 96–103
- Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Global Ecology and Biogeography 16:24–33
- Girvetz EH, Zganjar C, Raber GT, Maurer EP, Kareiva P, Lawler JJ (2009) Applied climate-change analysis: the climate wizard tool. Plos One 4:e8320. doi:10.137/journal.pone.0008320
- Glick P, Stein BA (eds) (2011) Scanning the conservation horizon: a guide to climate change vulnerability assessment. National Wildlife Federation, Washington, DC
- Graham RW, Lundelius EL Jr, Graham MA, Schroder EK, Toomey RS III, Anderson E, Baronsky AD, Burns JA, Churcher CS, Grayson DK, Guthrei RD, Harrington CR, Jefferson GT, Martin LD, McDonald HG, Morlan RE, Semken HA Jr, Webb SD, Werdelin L, Wilson MC (1996) Spatial response of mammals to late quaternary environmental fluctuations. Science 272:1601–1606
- Gray ST, Betancourt JL, Jackson ST, Eddy RG (2006) Role of multidecadal climate variability in a range extension of pinyon pine. Ecology 87:1124–1130
- Grayson DK (2005) A brief history of Great Basin pikas. Journal of Biogeography 32:2103–2111
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009
- Guralnick R (2007) Differential effects of past climate warming on mountain and flatland species distributions: a multispecies North American mammal assessment. Global Ecology and Biogeography 16:14–23

- Hamann A, Wang TL (2006) Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773–2786
- Hansen L, Hoffman J, Drews C, Mielbrecht E (2010) Designing climate-smart conservation: guidance and case studies. Conservation Biology 24:63–69
- Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology 12:2272–2281
- Holling CS (ed) (1978) Adaptive environmental assessment and management. Wiley, London
- Huntley B (1991) How plants respond to climate change-migration rates, individualism and the consequences for plant communities. Annals of Botany 67:15–22
- Illan JG, Gutierrez D, Wilson RJ (2010) The contributions of topoclimate and land cover to species distributions and abundance: fine-resolution tests for a mountain butterfly fauna. Global Ecology and Biogeography 19:159–173
- Jackson ST, Booth RK (2002) The role of Late Holocene climate variability in the expansion of yellow birch in the western Great Lakes region. Diversity and Distributions 8:275–284
- Jackson ST, Överpeck JT (2000) Responses of plant populations and communities to environmental changes of the Late Quaternary. Paleobiology 26(Suppl):194–220
- Jackson ST, Betancourt JL, Booth RK, Gray ST (2009a) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. Proceedings of the National Academy of Sciences of the United States of America 106:19685–19692
- Jackson ST, Gray ST, Shuman B (2009b) Paleoecology and resource management in a dynamic landscape: case studies from the Rocky Mountain Headwaters. In: Dietl GP, Flessa KW (eds) Conservation paleobiology: using the past to manage for the future. Paleontological Society Short Course, vol 15, 17 Oct 2009. The Paleontological Society Papers
- Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350
- Kearney M, Phillips BL, Tracy CR, Christian KA, Betts G, Porter WP (2008) Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. Ecography 31:423–434
- Keith DA, Akcakaya HR, Thuiller W, Midgley GF, Pearson RG, Phillips SJ, Regan HM, Araujo MB, Rebelo TG (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters 4:560–563
- Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. PNAS 105:11823–11826
- Lavergne S, Mouquet N, Thuiller W, Ronce O (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. Annual Review of Ecology, Evolution and Systematics 41:321–350
- Lawler JJ, White D, Neilson RP, Blaustein AR (2006) Predicting climate-induced range shifts: model differences and model reliability. Global Change Biology 12:1568–1584
- Lawler JJ, Shafer SL, White D, Kareiva P, Maurer EP, Blaustein AR, Bartlein PJ (2009) Projected climate-induced faunal change in the Western Hemisphere. Ecology 90:588–597
- Lawler JJ, Tear TH, Pyke C, Shaw MR, Gonzalez P, Kareiva P, Hansen L, Hannah L, Klausmeyer K, Aldous A, Bienz C, Pearsall S (2010a) Resource management in a changing and uncertain climate. Frontiers in Ecology and the Environment 8:35–43
- Lawler JJ, Shafer SL, Bancroft BA, Blaustein AR (2010b) Projected climate impacts for the amphibians of the Western Hemisphere. Conservation Biology 24:38–50

- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature 462:U1052–U1111
- Luoto M, Virkkala R, Heikkinen RK (2007) The role of land cover in bioclimatic models depends on spatial resolution. Global Ecology and Biogeography 16:34–42
- MacDonald GM, Bennett KD, Jackson ST, Parducci L, Smith FA, Smol JP, Willis KJ (2008) Impacts of climate change on species, populations and communities: palaeobiogeographical insights and frontiers. Progress in Physical Geography 32:139–172
- Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. Diversity and Distributions 15:59–69
- Martinez-Meyer E, Townsend Peterson A, Hargrove WW (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13:305–314
- Mawdsley JR, O'Malley R, Ojima DS (2009) A review of climatechange adaptation strategies for wildlife management and biodiversity conservation. Conservation Biology 23:1080–1089
- Merrill RM, Gutierrez D, Lewis OT, Gutierrez J, Diez SB, Wilson RJ (2008) Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. Journal of Animal Ecology 77:145–155
- Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151
- Monahan WB (2009) A mechanistic niche model for measuring species' distributional responses to seasonal temperature gradients. PLoS One 4(11):e7921
- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261–264
- Moss RH, Edmonds JA, Hibbard KA, Manning MR, Rose SK, van Vuuren DP, Carter TR, Emori S, Kainuma M, Kram T, Meehl GA, Mithchell JFB, Nakicenovic N, Riahi K, Smith SJ, Stouffer RJ, Thomson AM, Weyant JP, Wilbanks TJ (2010) The next generation of scenarios for climate change research and assessment. Nature 463:747–756
- Myers P, Lundrigan BL, Hoffman SMG, Haraminac AP, Seto SH (2009) Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. Global Change Biology 15:1434–1454
- Neely B, McCarthy P, Cross M, Enquist C, Garfin G, Gori D, Hayward G, Schulz T (2010) Climate change adaptation workshop for natural resource managers in the Gunnison Basin: summary. Southwest Climate Change Initiative, The Nature Conservancy
- Niven DK, Butcher GS, Bancroft GT, Monahan WB, Langham G (2009) Birds and climate change: ecological disruption in motion. a briefing for policymakers and concerned citizens on audubon's analyses of North American bird movements in the face of global warming. http://birdsandclimate.audubon.org/ techreport.html. Accessed 9 Nov 2009
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. The Annual Review of Ecology, Evolution and Systematics 2006:637–669
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42
- Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Laila L, Kulberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583

- Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81:443–450
- Pearman PB, Guisan A, Borennimann O, Randin CF (2008) Niche dynamics in space and time. Trends in Ecology and Evolution 23:149–158
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371
- Pearson RG, Thuiller W, Araujo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC (2006) Model-based uncertainty in species range prediction. Journal of Biogeography 33:1704–1711
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102–117
- Peterson AT, Ortega-Huerta MA, Bartley J, Sanchez-Cordero V, Soberon J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. Nature 416:626–629
- Peterson GD, Cumming GS, Carpenter SR (2003) Scenario planning: a tool for conservation in an uncertain world. Conservation Biology 17:358–366
- Rodder D, Schmidtlein S, Veith M, Lotters S (2009) Alien invasive slider turtle in unpredicted habitat: a matter of niche shift or of predictors studied? Plos One 4(11):e7843
- Rodenhuis DR, Bennett KE, Werner AT, Murdock TQ, Bronaugh D (2009) Hydro-climatology and future climate impacts in British Columbia. Pacific climate impacts consortium. University of Victoria, Victoria 132 pp
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60
- Rosenzweig C et al (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453:U320– U353
- Rowe RJ, Finarelli JA, Rickart EA (2010) Range dynamics of small mammals along an elevational gradient over an 80-year interval. Global Change Biology 16:2930–2943
- Salazar K (2009) Secretarial order no. 3289: Addressing the impacts of climate change on America's water, land, and other natural and cultural resources. In: DOI (ed.), Washington, DC
- Santa Clara University, Bias Corrected and Downscaled WCRP CMIP3 Climate Projections (2010) http://gdo-dcp.ucllnl.org/ downscaled_cmip3_projections/. Accessed 14 Jan 2010
- Schauffler M, Jacoboson GL (2002) Persistence of coastal red spruce refugia during the Holocene in northern New England, USA, detected by stand-scale pollen stratigraphies. Journal of Ecology 90:235–250
- Solomon SD, Quin D, Manning M, Alley RB, Berntsen T, Bindoff NL (2007) Technical summary. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Climate change 2007: the physical science basis. Contributions of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge
- Southwest Climate Change Network (2010) http://southwestclimate change.org/climate. Accessed 8 Jan 2010
- Sutherst R, Floyd RB, Maywald GF (1995) The potential geographical distribution of the Cane Toad, Bufo marinus L in Australia. Conservation Biology 9:294–299
- Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland response to changing climate. Science 315:640–642

- Swetnam TW, Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climate 11:3128–3147
- Theobold DM (2004) Placing exurban land-use change in a human modification framework. Frontiers in Ecology and the Environment 2:139–144
- Thuiller W, Brotons L, Araujo MB, Lavorel S (2004) Effects of restricting environmental range data to project current and future species distributions. Ecography 27:165–172
- Thuiller W, Lavorel S, Araujo MB (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography 14:347–357
- Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences of the United States of America 106:19637–19643
- Urban MC, Phillips BL, Skelly R, Shine (2007) The cane toad's (*Chaunus [Bufo] marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. Proceedings of the Royal Society B 274:1413–1419
- U.S. Environmental Protection Agency (US EPA) (2009) A framework for categorizing the relative vulnerability of threatened and endangered species to climate change. National Center for Environmental Assessment, Washington, EPA/600/R-09/011
- U.S. Fish and Wildlife Service (USFWS) (2010) Rising to the urgent challenge: Strategic plan for responding to accelerating climate change. http://www.fws.gov/home/climatechange/strategy.html
- Varela S, Rodriguez J, Lobo JM (2009) Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. Journal of Biogeography 36:1645–1655
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395
- West JM, Julius SH, Kareiva P, Enquist E, Lawler JJ, Petersen B, Johnson AE, Shaw MR (2009) U.S. natural resources and climate change: concepts and approaches for management adaptation. Environmental Management 44:1001–1021
- Wiens JA, Bachelet D (2010) Matching multiple scales of conservation with the multiple scales of climate change. Conservation Biology 24:51–62
- Wiens JA, Stralberg D, Jongsonmijt D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. Proceedings of the National Academy of Sciences 106:19729–19736

Wildland-Urban Interface Maps (2010) http://www.silvis.forest.wisc. edu/projects/WUI_Main.asp. Accessed 8 Feb 2010

- Williams JW, Jackson ST, Kutzbacht JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America 104:5738–5742
- Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. Plos Biology 6:2621–2626
- Williams JE, Haak AL, Neville HM, Colyer WT (2009) Potential consequences of climate change to persistence of cutthroat trout populations. North American Journal of Fisheries Management 29:533–548
- Willis KJ, Birks HJB (2006) What is Natural? The need for a long-term perspective in biodiversity conservation. Science 314:1261–1265
- Young B, Byers E, Gravuer K, Hall K, Hammerson G, Redder A (2009) Guidelines for using the NatureServe climate change vulnerability index, Release 1.0. http://www.natureserve.org/ prodServices/climatechange/ClimateChange.jsp#v1point2. Accessed 25 Feb 2010