Issues and Perspectives — Invited

Tools for Assessing Climate Impacts on Fish and Wildlife

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Abstract

Climate change is already affecting many fish and wildlife populations. Managing these populations requires an understanding of the nature, magnitude, and distribution of current and future climate impacts. Scientists and managers have at their disposal a wide array of models for projecting climate impacts that can be used to build such an understanding. Here, we provide a broad overview of the types of models available for forecasting the effects of climate change on key processes that affect fish and wildlife habitat (hydrology, fire, and vegetation), as well as on individual species distributions and populations. We present a framework for how climate-impacts modeling can be used to address management concerns, providing examples of model-based assessments of climate impacts on salmon populations in the Pacific Northwest, fire regimes in the boreal region of Canada, prairies and savannas in the Willamette Valley-Puget Sound Trough-Georgia Basin ecoregion, and marten *Martes americana* populations in the northeastern United States and southeastern Canada. We also highlight some key limitations of these models and discuss how such limitations should be managed. We conclude with a general discussion of how these models can be integrated into fish and wildlife management.

Keywords: climate change; ecological modeling; hydrology; vegetation; fire

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Editor's Note: Dr. Kurt Johnson (kurt_johnson@fws.gov) served as the Guest Editor and invited this themed paper (along with several others, to be published in subsequent issues) focused on assessing impacts and vulnerability of fish and wildlife to accelerating climate change.

Introduction

Climate change has the potential to greatly alter fish and wildlife populations and their habitats (Parry et al. 2007). Increasing temperatures and altered precipitation patterns are likely to affect species distributions as well as hydrological cycles, fire regimes, and vegetation communities. In many cases, successful fish and wildlife management will require proactive measures to address climate change. To develop these measures, managers will need a basic understanding of the ways in which ecological systems are likely to respond to climate change (Littell et al. 2011). Models that project the potential ecological effects of climate change will play a critical role in providing such an understanding. Specifically, these models can contribute to climate change vulnerability assessments, aid in the development of climate change adaptation strategies, and help in setting management priorities and goals as part of a larger and iterative planning and decision-making process (Figure 1).

Here, we provide an overview of some of the types of models that can be used to project the effects of climate change on ecological systems (summarized in Table 1), and we describe a framework for the effective use of models (Box 1). We begin with a brief discussion of climate models. We then focus on four areas of climate impacts that are critical to fish and wildlife habitat and population management: hydrology, fire, vegetation, and individual species responses. We describe the types of models that are available, discuss model limitations, and provide examples of model applications. We develop some of those examples into case studies in which we describe the methods and model interpretation in greater detail and apply a simple climate-impacts modeling framework. We conclude by making recommendations for incorporating climate-impacts modeling into fish and wildlife management, being careful to consider the limitations of existing tools. This review is a general introduction to modeling tools for projecting climate impacts. It does not provide a comprehensive review of the history or the state-of-the-art in any of the four fields of modeling. Instead, it is meant to be an accessible overview of how ecological models can potentially contribute to climate-impacts assessments.

Modeling Approaches

Climate models

General circulation models (GCMs) are numerical models that simulate the physical processes of climate. These models are the complex dynamic models upon which the Intergovernmental Panel on Climate Change (IPCC) has based many of its conclusions and whose outputs biologists and modelers in other fields have used to forecast potential ecological climate impacts. The GCMs used in the IPCC Fourth Assessment Report (IPCC AR4) were coupled atmosphere–ocean general circulation models that incorporate processes of thermal energy storage and release in the oceans as well as the atmosphere (Solomon et al. 2007). Most of these models included sea–ice dynamics and an interactive land–surface component with hydrologic effects, and some included effects of simulated vegetation. The complexity of these models derives from the physical equations used to calculate the movement of mass, momentum, and energy through the climate system and the multiple layers of the atmosphere and ocean for which energy inputs and outputs are calculated. A very simple climate model might include three layers—the sun and outer space, the Earth's atmosphere, and the Earth's surface—and model three atmospheric processes: solar radiation, thermal radiation, and absorption. The greenhouse effect is an emergent property of this system in which thermal radiation from the Earth's surface is absorbed by the atmosphere and re-radiated back toward the Earth, maintaining the surface temperature within a range suitable for life. General circulation models explicitly model energy transfer processes such as the greenhouse effect and include many more mechanisms of climate

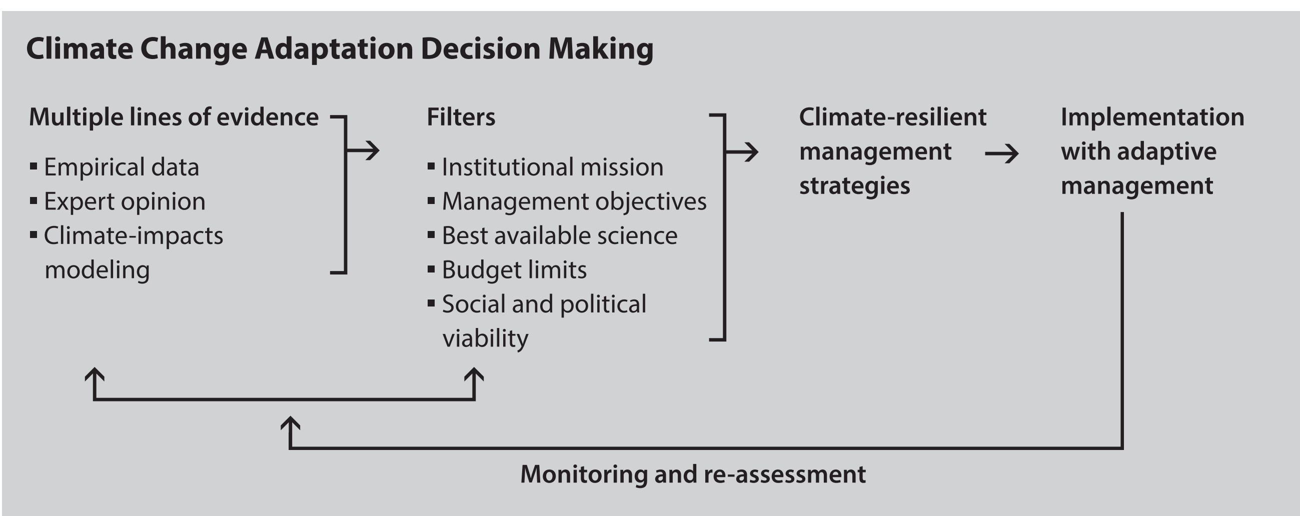

Figure 1. Integration of climate-impacts modeling into an iterative decision-making process whose goal is to implement and evaluate climate-resilient management strategies.

Box 1: **A framework for climate-impacts modeling**

Phase I: Project Scoping

1. Define management questions
2. Define spatial scale and timeframe
3. Assemble relevant data
4. Identify key ecological processes

Phase II: Modeling

1. Select and/or build models
2. Select or develop scenarios
3. Run models

Phase III: Summary and Interpretation

1. Summarize outputs targeting management questions
2. Characterize uncertainty
   a. across climate models
   b. due to parameter values
   c. reflecting scenarios

Effective climate-impacts modeling occurs within a broader decision-making process that identifies the management question and defines the spatial scale and timeframe of interest. Assembling relevant data can include identifying modeling studies that have already been completed (including downscaled climate data) or looking for empirical data to parameterize a new model.

Identifying the dominant ecological process along with the scale and timeframe determines the type of climate-impacts model used (e.g., hydrological, fire, vegetation, or individual species). Model complexity may also be a factor when building a model yourself. Scenario development is critical and should consider the original management question as well as capture future uncertainty.

Selecting outputs that target the original management question improves the interpretation of results. It is important to characterize uncertainty in model outputs, whether across climate models, future scenarios, or resulting from uncertainty in the parameterization of the model itself.

forcing and feedback. A forcing is any model input that directly impacts either the amount of solar radiation reaching the Earth's surface or the amount of thermal radiation exiting to space (Hartmann 1994). Forcings may be natural, such as aerosols of volcanic origin, or anthropogenic, such as increases in greenhouse gases due to the burning of fossil fuels. Climate feedbacks respond to changes in global mean temperature and also directly or indirectly affect the Earth's solar and thermal radiation budgets (Bony et al. 2006). Examples of feedbacks include humidity (warmer air holds more water vapor, a greenhouse gas that contributes to further warming), clouds (may result in warming or cooling depending on the cloud type), and ice– and land–surface albedo (melting ice results in additional warming because ice cools the Earth's surface by reflecting incoming solar radiation).

Limitations and uses. Variability in climate projections provides a significant challenge for modeling ecological climate impacts. Climate sensitivity is a standardized measurement used to quantify this variability. It is the change in global mean temperature that occurs when the global average surface air temperature reaches equilibrium in response to a doubling of atmospheric CO_2 (Bony et al. 2006). Projections of climate sensitivity range from 2.0 to 4.5° C (Solomon et al. 2007), but they may be significantly higher than this projection (Roe and Baker 2007). Some of this variability stems from variation in GCM structures and inputs. Each of the 23 GCMs involved in the IPCC AR4 simulates climate processes differently, producing different projections of future climates (Solomon et al. 2007). Gaps in our understanding of the climate system also generate uncertainty. For example, GCMs are currently unable to accurately simulate precipitation (especially in the tropics), oceanic oscillations, and cloud dynamics (Solomon et al. 2007). Forcing components are also a source of uncertainty in GCM projections, particularly the effect of aerosols and greenhouse-gas emissions (Solomon et al. 2007). Finally, the different greenhouse-gas emissions scenarios used to define anthropogenic forcings in GCMs result in a range of projections. For continental- or global-scale projections or for more than about two decades into the future, greenhouse-gas emission scenarios and GCM structure are the two greatest sources of variability in climate projections (Hawkins and Sutton 2009, 2011). The differences in emissions scenarios account for the greatest amount of variation in projections farther than about 50 y into the future. In subcontinental and regional projections of the next one or two decades, internal variability in model runs (i.e., climatic variability) is the primary source of uncertainty, followed by variability due to GCM structure (Hawkins and Sutton 2009). Improved understanding and validation of climate feedback mechanisms may further reduce uncertainties in projected climate sensitivities (Bony et al. 2006) and improve confidence in short-term regional projections, but they are unlikely to alter long-term global projections (Hawkins and Sutton 2009) or reduce the occurrence of extreme projections (Roe and Baker 2007).

General circulation model resolution is often too coarse (15,000–25,000 km^2) for outputs to be used directly by regional or local climate-impacts models (Solomon et al. 2007). Therefore, projections must be downscaled to finer resolutions, either statistically or dynamically. Statistical downscaling translates climate projections to a finer scale (1–50 km^2) grid cells or a single site by using statistical relationships based on historical climate records, topography, or both (Salathe et al. 2007). General circulation model outputs also can be downscaled dynamically with regional climate models (RCMs). These models are similar to GCMs, but they model dominant regional climate mechanisms at finer scales ($<$20 km^2). Generally, RCMs differ from statistical downscaling because they model drivers of local climate explicitly (Salathe et al. 2007; Solomon et al. 2007). However, RCMs can be as difficult to build and time-consuming to run as GCMs. Both statistical and dynamic (e.g., RCM) downscaling methods introduce additional uncertainty in climate projections. Statistically and dynamically downscaled climate projections have been made publicly available at resolutions ranging from 1 to 50 km^2 (e.g., Maurer et al. 2007; Ramirez and Jarvis 2008; Girvetz et al. 2009; Mearns et al. 2009) at regional and global scales, so that ecological and other climate-impacts modelers can avoid the task of manipulating the raw GCM output or performing the downscaling.

Comparative studies of output across multiple GCMs coordinated by the Coupled Model Intercomparison Project (Meehl et al. 2007; CMIP 2010) found that projected changes in decadal mean surface temperatures are most informative at approximately 40 y into the future and noisier with increasing latitude (Hawkins and Sutton 2009). This finding has led, in part, to a new emphasis on decadal prediction that may increase the availability of medium-term (10–30 y) regional climate projections (Meehl et al. 2009) and is integrated into the latest Coupled Model Intercomparison Project 5 (Taylor et al. 2012). When studying longer term projections, out 100 y or more, an explicit characterization of uncertainties becomes more important, typically by using an ensemble of GCM simulations (e.g., Mote et al. 2011). Ensembles combine projections from multiple GCMs, emissions pathways, or a combination (Tebaldi and Knutti 2007; Knutti et al. 2010) and can help quantify the variability and inherent uncertainty in future climate projections (e.g., Garcia et al. 2012).

In spite of the many known uncertainties described above, the climate projections produced by GCMs and RCMs are useful for assessing ecological climate impacts. The strength of the GCMs lies in their foundation in physical principles (as opposed to applying purely statistical projections), and their robustness is evident in their ability to recreate broad patterns of climate variability and simulate past climates (Solomon et al. 2007). The latest generation of coupled atmosphere–ocean general circulation models and Earth System Models that include carbon cycling (e.g., http://www.cesm.ucar.edu) are a promising improvement. They include advances in simulations of important phenomena such as the El Niño Southern Oscillation (Guilyardi et al. 2012), and they outperform the previous generation of GCMs in their ability to simulate historical temperature changes at fine spatial and temporal scales (Sakaguchi et al. 2012). Despite these models representing more processes in greater detail and including more explicit feedback mechanisms, the variation among model projections has not increased (Knutti and Sedlacek 2012).

There have been many attempts to guide the selection of which GCMs should be included in a particular impacts study (e.g.,Tebaldi and Knutti 2007). However, using the ability of GCMs to reproduce historical climate (i.e., model skill) to rank models is difficult to implement consistently (Knutti et al. 2010; Weigel et al. 2010). The magnitude of projected impacts has generally shown little dependence on the skill of the GCMs included in an ensemble (e.g., Brekke et al. 2008; Pierce et al. 2009). So, it is unclear whether the ability to simulate past conditions results in greater certainty in future forecasts, leading to the common conclusion that model skill may be less important in estimating climate change impacts as long as a large ensemble of GCMs is used (Mote et al. 2011).

Hydrological models

Among other things, hydrological models can simulate climate-driven changes in the timing and quantity of stream flow, snowpack dynamics, and evapotranspiration, all factors with potential to influence fish and wildlife populations both directly and through indirect effects on habitat suitability. Model outputs can be useful for developing land-management policy. For example, projected downstream impacts of climate change on freshwater species may support upstream habitat restoration or land-use planning, particularly when model outputs suggest future increases in extreme hydrological events, such as drought and flooding. Outputs from hydrological models also provide inputs to other climate-impacts models, including fire and vegetation models.

There are a wide variety of hydrological models, and they differ in their structure and application (Kampf and Burges 2007). Most hydrological models include equations that account for the major components of water and energy budgets as well as a flow-routing scheme to redistribute water through a catchment. Spatially explicit hydrological models divide the study area into discrete elements, such as a regular grid. Meteorological data are passed to each grid cell, and the model produces estimates of important hydrological variables such as runoff, evaporation, and snowpack. Runoff is typically routed through a river network to produce flow estimates at strategic points.

Coarse-scale (15,000–25,000 km^2), one-dimensional hydrological models are embedded in many GCMs. These models can be used to examine global patterns of runoff and soil moisture, but they have trouble simulating historical flows because they are one-dimensional and therefore lack routing in two-dimensional space (Parry et al. 2007). The coarse resolution of GCMs and runoff-estimate biases make these models difficult to use at subcontinental scales.

Macroscale hydrological models (e.g., Liang et al. 1994) are typically applied at grid resolutions that range from 4 to 25 km. They generally represent hydrological processes in more detail than GCM-embedded models (Cherkauer and Lettenmaier 2003). Macroscale models also can be driven by weather station data, regional climate model output, or statistically downscaled GCM output.

Table 1. Types of climate-impacts models, their potential applications and limitations. Information adapted from reviews by Keane et al. (2004), Botkin et al. (2007), Kampf and Burgess (2007), Solomon et al. (2007), Flannigan et al. (2009), Lawrence et al. (2011), Littell et al. (2011), and Seidl et al. (2011).

Ecological process	Model categories	Description	Applications	Limitations
Climate (Solomon et al. 2007)	Global climate models (GCMs)	Coupled AOGCM[a] simulate movement of mass, momentum, and energy through layers of the atmosphere and ocean	Estimate climate sensitivity Project global and regional changes in temperature, precipitation, and other aspects of climate	Coarse spatial resolution Variability among GCMs Uncertainty around modeling of climate feedback mechanisms Inability to capture regional climate phenomena
	Regional climate models	Dynamic downscaling of GCM output simulating regional climate phenomena	Estimate regional projected changes in temperature, precipitation, and other measures of climate Provide inputs to other climate-impacts models	Variability among GCMs Uncertainty associated with modeling regional processes
	Downscaled GCM output	Statistically downscale GCM output based on historical climate, topography, or both	Same as regional models	Variability among GCMs Finer spatial resolution does not imply the inclusion of regional climate processes
Hydrological (Kampf and Burgess 2007)	Global climate models	One-dimensional empirical models of runoff and soil moisture	Continental-scale patterns of runoff and soil moisture	Coarse spatial resolution One-dimensional representation Uncertainty in precipitation projections
	Macroscale hydrological models	Two-dimensional models incorporating soil moisture, runoff, and flow routing (4–25-km grid cell size)	Global and subcontinental patterns of runoff and soil moisture Drought and flow forecasting Hydropower planning Impacts of land-use change	Uncertainty in precipitation projections May not include changes in land-use, disturbance, and vegetation cover
	Subregional hydrological models (also see coupled hydrological-vegetation models)	Including more processes than macroscale, such as groundwater movement and effects of shading and vegetation Fine resolution (can be $<$100 m)	Impacts of land-use change (e.g., forestry and restoration) Potential for erosion and mass wasting Valuation of ecosystem services	Uncertainty in precipitation projections and changes in land cover Improved representation of local processes requires more data and time to parameterize and run the model
Fire (Keane et al. 2004; Flannigan et al. 2009; Seidl et al. 2011)	Fire hazard and fire weather models	Empirical index of fire risk based on present and future fuel availability and weather conditions suitable for fire	Detect change in fire danger, season length, potential fire behavior, and resulting haze	Static models of current conditions Limited by the resolution of model inputs (e.g., characterization of fuels) and uncertainty in precipitation projections
	Fire occurrence and area burned models	Empirical model relating meteorological variables to fire occurrence or historical area burned	Estimate area burned and fire frequency Identify sites for management Estimating future wildfire suppression costs	Assume that past climate and fire relationships will continue in the future Do not consider feedbacks between vegetation and fire
	Fire behavior and effects models	Process-based models simulate fire spread and impacts on a real or representative landscape	Stand level Estimate fire effects including area burned, mortality, age-class distribution, smoke, and soil heating	Rely upon historical relationships for specification of key parameters, such as ignition probabilities and fire severity, for each vegetation types
	Landscape fire succession models (also see landscape models)	Process-based models simulate fire behavior and effects as well as vegetation succession	Spatially explicit estimates of fire regime, fire season length, area burned, carbon flux, mortality, age-class distribution, fire effects, and vegetation succession	Rely upon historical relationships for specification of key parameters, such as ignition probabilities and fire severity, for each vegetation types Complex models difficult to learn

Table 1. Continued.

Ecological process	Model categories	Description	Applications	Limitations
Vegetation (Lawrence et al. 2011; Littell et al. 2011)	Forest gap models	Simulate forest dynamics at the stand or patch level	Simulated forest species composition, biomass, seed dispersal, and stem density	Stand-level projections Impacts of increased CO_2 on WUE[b] across life stages still poorly understood Some processes (e.g., grazing and disease) may be left out of models Absence of future land-use change
	Landscape models	Simulate multiple processes (e.g., management, disturbance, competition, and dispersal) occurring at the scale of the landscape, stand, species, and individual tree	Simulated forest species composition, biomass, and disturbance regimes	Impacts of increased CO_2 on WUE across life stages still poorly understood Complex models difficult to learn
	Dynamic global vegetation models	Simulate percent cover of globally distributed plant functional types	Simulate growth and disturbance (including fire), percent cover of plant functional types, and seed dispersal	Simulate a limited number of plant functional types Often unable to simulate individual stands Impacts of increased CO_2 on WUE across life stages still poorly understood Complex models difficult to learn
	Biogeochemical models	Simulate forest–atmosphere processes (e.g., gas exchange and hydrology) and carbon and nutrient budgets	Used to identify rate- and process-limiting factors across biomes or geographic regions Track multiple processes such as changes in net primary productivity, abiotic soil processes, and nutrient cycles	Based on plant functional types rather than species Input variables not readily available Highly technical and difficult to learn
	Coupled hydrological vegetation models	Simulates hydrologic, biogeochemical, and vegetation processes	Simulate stream flow, net primary productivity, nutrient cycling, and dynamic land cover in responses to variation in topography, vegetation, and climate Often embedded in global or regional climate models	Uncertainty in precipitation projections Limited number of plant function types or land cover classes Uncertainty in parameterization of complex biogeochemical processes and feedbacks Highly technical and difficult to learn
Individual species (Botkin et al. 2007)	Empirical and statistical models	Use statistical or algorithmic techniques to relate historical climate to current species' distributions	Model range contractions and expansions Identify threatened species Highlight areas for conservation action	Assume that the current distribution represents the climatic limit of the species Does not consider phenotypic plasticity or evolution, dispersal ability, interspecific interactions, or varying climate tolerances across life stages Projections vary across modeling approaches
	Mechanistic models	Spatially explicit population models Cellular automata Connectivity models Bioenergetic models	Simulate population abundance and dynamics, dispersal, gene flow, phenology, connectivity, range contractions, and expansions Identify threatened species Cumulative impacts assessment	Complex models with many, sometimes unknown, parameters can introduce uncertainty Time-consuming to build and run simulations

[a] AOGCM = atmosphere–ocean global climate model.
[b] WUE = water-use efficiency.

Macroscale models are often used to examine how climate affects the hydrologic cycle at continental and subcontinental scales (e.g., Maurer 2007).

Subregional hydrological models (e.g., Wigmosta et al. 1994) represent terrain at finer resolutions (i.e., $<$100 m) and may contain more processes than macroscale models, such as lateral distribution of groundwater, shading in areas of high topographic relief, or vegetation effects. Subregional models also are driven by meteorological data, although the data must often be interpolated. Subregional models are appropriate for simulating the effects of climate and land use on the hydrology of small catchments, for which representing topographic complexity is important.

Limitations and uses. Hydrological models are limited by uncertainties in the parameterization of underlying physical equations, model structure, and model inputs, such as climate data and land–surface parameterizations (Parry et al. 2007). These models are particularly sensitive to uncertainties in precipitation data, the primary driver of hydrology. Precipitation is difficult to measure and is sparsely measured (e.g., one National Oceanic and Atmospheric Administration cooperative observer station per $\sim$700 km^2; Maurer et al. 2002), leading to uncertainties in the characterization of spatial distribution of precipitation used to force a hydrological model. Projections of future precipitation carry the additional uncertainties related to emission scenarios (Christensen et al. 2007), GCMs (Graham et al. 2007), and downscaling (Fowler et al. 2007). Because future temperature projections are generally more consistent among GCMs than precipitation projections, modeled hydrologic impacts driven by temperature, such as changes to snow-dominated basins (e.g., McKelvey et al. 2011), are less variable than impacts that are driven by precipitation.

Nonclimatic factors influence hydrology and may complicate interpretation of simulations if not included in a model. Land-use change, including climate-induced vegetation change, may alter hydrology as much as climate change (Parry et al. 2007). For example, the tree line may shift upward in elevation with warming (Harsch et al. 2009), and wildfires may increase in size and frequency in response to warmer, drier conditions (Littell et al. 2009; Littell and Gwozdz 2011). A warmer, drier climate also could increase irrigation demand such that even when coupled with more efficient irrigation technologies, in-stream flows could be reduced. Changes in agriculture, irrigation practices, and reservoir operation are as likely as climate-induced change, and previous study shows that such changes can affect model results (Haddeland et al. 2007). These additional factors are often addressed in a separate model that uses hydrological model output to assess water-system changes (e.g., Vicuna et al. 2007). Dynamic vegetation responses, such as effects of increased CO_2 concentrations on biomass production and transpiration rates, can be important at the continental scale (Betts et al. 2007). However, these vegetation responses are rarely included in hydrological models because their hydrologic impact is considered substantially smaller than climate or land use (Piao et al. 2007; but see Lawrence et al. 2011).

Hydrological models are useful for developing adaptation strategies to address climate change. Macroscale models have been used for land-management impact assessment (e.g., Haddeland et al. 2007) and mapping of suitable wolverine *Gulo gulo* habitat based on projected spring snowpack (McKelvey et al. 2011). Subregional models have been used to test the effect of land-use change and forestry practices on flows (e.g., VanShaar et al. 2002) and to compare the impact of climate and habitat restoration on salmon populations (e.g., Battin et al. 2007). Selecting the right model to address the spatial scale of interest is crucial, but it often involves balancing accuracy with cost while ensuring the model is capable of simulating the most important aspects driving local ecosystem impacts. Models are constantly evolving to simulate more aspects of the environment driving or responding to hydrologic change, such as urban and agricultural water management (e.g., Yates et al. 2005), sediment production and transport (e.g., Doten et al. 2006), and stream temperatures (e.g., Ficklin et al. 2012). Subregional hydrological models may be necessary for capturing local-scale dynamics and climate-induced impacts not captured by coarse-resolution models. However, a subregional model requires additional time to parameterize, calibrate, and run compared with the simpler process of setting up and running a macroscale model, and many macroscale models do have the ability to account statistically for subgrid scale variability in elevation, rainfall, or other characteristics. Greater availability of downscaled climate data may increase the use of subregional hydrological models. Climate change adaptation strategies for freshwater systems will benefit from hydrological modeling projections that characterize the direction, magnitude, and uncertainty of future change as well as evaluate the benefits of proposed management.

Case study. Changing river flow rates can have significant ecological consequences. Flow rates influence the extent of available freshwater habitat, mediate changes in habitat condition over time, regulate the input and output of nutrients and waste, and can restrict habitat connectivity (Rolls et al. 2012). Assessing the consequences of altered flows on species of management concern is therefore a high priority for the conservation of freshwater species and ecosystems. Furthermore, identifying areas in which habitat preservation or restoration may mitigate these changes is needed for climate change adaptation.

Battin et al. (2007) linked climate, hydrological, land-use, and wildlife population models to assess the effects of climate change on habitat restoration for Chinook salmon *Oncorhynchus tshawytscha* (Box 2). The system of linked models allowed the researchers to simultaneously consider scenarios for both climate change and habitat restoration and to assess their relative impact on salmon abundance. Battin et al. (2007) found that climate change is likely to impact both peak winter and minimum summer flows, with potential negative impacts on salmon recruitment that outweigh gains from habitat restoration in most places. They addressed uncertainty by using outputs from two GCMs and two habitat

Box 2
Projected impacts of climate change on salmon habitat restoration
(Battin et al. 2007)

Phase I: Project Scoping

Watershed restoration often includes improving habitats for threatened and endangered aquatic species (Bernhardt et al. 2005). Battin et al. assessed how climate change may affect the benefits of habitat restoration for salmon populations in the Snohomish River Basin, WA, USA. The timeframe of interest was early- (2025) and mid-century (2050). They made use of an existing spatially explicit salmon population model (Shiraz, Scheuerell et al. 2006) whose design allowed them to explore the impacts of stream flow on salmon recruitment and abundance.

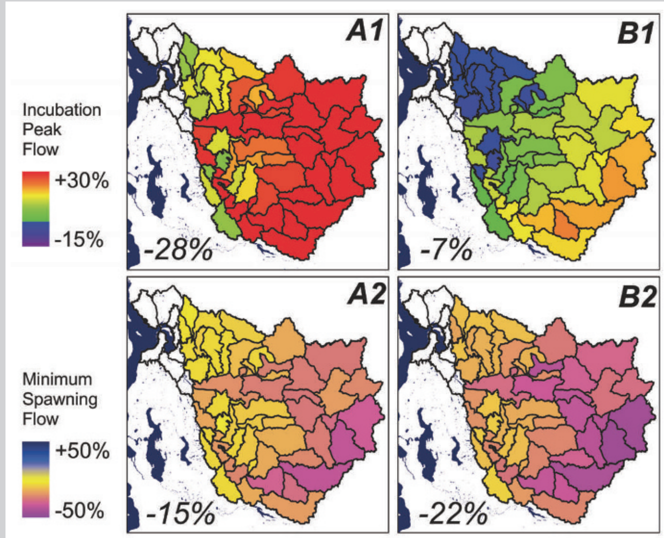

Figure 2-1. *Percent increased stream flow in the Snohomish River Basin, WA. Flow results from hydrological simulations in the Snohomish River Basin (Battin et al. 2007). Output is aggregated across sub-basins which are delineated by black lines. Simulations were driven by two general circulation models (A and B) assuming a single CO_2 emission scenario. Incubation peak flows occur from October 15 to February 15. Minimum spawning flows occur from September 15 to November 15. Adapted from Battin et al. (2007). Copyright (2007) National Academy of Sciences, U.S.A.*

Phase II: Modeling

Salmon recruitment is sensitive to stream flow. Therefore, Battin et al. drove a coupled hydrological-vegetation model (Wigmosta et al. 1994) with climate projections from two general circulation models run under a single CO_2 emission scenario. The coupled model allowed them to incorporate the impacts of forest restoration on stream flow, and they modeled three predicted habitat restoration scenarios. Outputs from the hydrological model were used to drive the salmon population model.

Phase III: Summary and Interpretation

Hydrological simulations indicated that climate change may alter flow regimes in a large number of Snohomish River sub-basins during sensitive periods of the salmon lifecycle (Figure 2-1). The magnitude and spatial pattern of change in incubation peak flows (A1 and B1) varied greatly between general circulation models, highlighting uncertainties in projected precipitation. The spatial pattern and magnitude of decline in minimum flows (A2 and B2) during the spawning period varied less between models. Population simulations suggest that climate impacts will generally overwhelm recovery efforts for the species, but that restoration in low-elevation areas will be most effective (results not shown).

restoration scenarios, but they used only a single CO_2 emissions scenario because variability among emissions scenarios is modest in 25- and 50-y projections. Hydrological outputs from the two GCMs agreed on the simulated magnitude and spatial pattern of change in summer minimum flows, but they differed for winter peak flows. Given these uncertainties, Battin et al. (2007) suggested focusing on downstream portions of the watershed with greater model agreement and less projected change. These downstream areas had fewer simulated declines in salmon populations under all scenarios. A focus on the restoration of low-elevation sites for their potential resilience to climate change is a strategy that may apply to other basins supporting salmon populations or other fish populations sensitive to flow rates.

Fire models

Fire is an essential ecological process affecting nutrient cycling, regulating the density of young trees and the redistribution of water and sediment, and creating habitat for fish and wildlife (Noss et al. 2006). Widespread changes in these processes may alter the habitat and food sources for entire wildlife communities, in some cases reducing habitat availability and connectivity.

Fire–climate models estimate the effects of climatic variability and change on components of fire regimes, including frequency, extent, severity, seasonality, and spatial pattern. These models can be empirical (e.g., based on correlative relationships derived from current or historical patterns; Flannigan et al. 2005), process-based (e.g., based on rules or functions that together simulate one or more processes; Andrews et al. 2004), or some combination of the two (Keane et al. 2004), and they have been used at many spatial and temporal scales (Flannigan et al. 2009). Given the critical role that fire plays in shaping the composition and distribution of vegetation, understanding the effects of climate change on fire regimes will be critical for wildlife management.

Fire is a contagious disturbance process that spreads across a landscape based on local weather and the spatial connectivity of fuels (Peterson 2002; McKenzie et al. 2011). Climate drives fire regimes through the short-term effects of weather on fuel moisture and the long-term effects of climate on vegetation growth and distribution. Vegetation patterns combine with climate and topography to influence fire regimes (Swetnam and Betancourt 1998) whose pattern, severity, and seasonality then strongly influence vegetation composition and structure (Lenihan et al. 2008). Viewed at coarse scales (e.g., subcontinental regions), fire is driven by climate (Littell et al. 2009). At finer scales (e.g., a watershed or forest stand), fuel loads and topography can have substantial effects, except under extreme weather conditions (Turner and Romme 1994). Consequently, coarse-scale fire models tend to be empirical models of fire weather, occurrence, or area burned based on the climatic conditions that drive extreme weather events (Lenihan et al. 2008). Fine-scale process-based models, including models of fire behavior and landscape succession models, often take a wider array of inputs, including vegetation structure and available fuels, topography, and ignition sources, in combination with climate-driven weather.

The temporal scale of a study also influences which processes are included in process-based simulation models and which variables are used for empirical models. For example, short-term dynamic predictions of fire behavior and fire effects usually simulate fire spread combined with calculations of consumption, smoke emissions, and plant mortality (Keane et al. 2003). Long-term projections can be based on empirical models derived from paleo-fire records (Higuera et al. 2009) and climate reconstructions, 20th century meteorological and fire observations (Littell et al. 2009), or multidecadal simulations that couple GCM outputs with a dynamic vegetation model that includes a fire module (Lenihan et al. 2008).

Among the most integrative modeling approaches are the so-called landscape fire succession models that combine process-based simulation methods with empirical relationships between climate and fire, to project the impacts of climate on vegetation, fire, and their interaction (Keane et al. 2004). These models typically produce spatially explicit estimates of vegetation succession, fire ignitions, fire spread (area burned), and fire effects (e.g., mortality, consumption, smoke, and soil heating), but they come in many forms and vary widely in complexity (Keane et al. 2004). There are four general components of the ideal landscape fire succession model: 1) ecological processes; 2) climate dynamics; 3) disturbance interactions; and 4) spatially explicit structure and process, but no models currently in use have all of these components (R. E. Keane, USDA Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory, personal communication). More sophisticated landscape fire succession models—particularly those that are to be applied to mountainous and semiarid landscapes—could incorporate topographically relevant hydrological models.

Limitations and uses. One of the largest limitations of using empirical models to predict future fire regimes is the assumption that historical relationships among climate, fuels, and fire will hold in the future. Novel climates, new vegetation communities, and future management policies may alter many of these historical relationships, particularly at finer spatial scales (McKenzie and Littell 2011). Process-based simulation models are similarly limited by their reliance on historical relationships for the specification of key fire-regime parameters, such as distributions of ignition probabilities and metrics of fire severity for specific vegetation types. Furthermore, process-based models vary in the extent to which human impacts, such as ignition probabilities, or the impacts of other natural disturbances, such as insect outbreaks and plant disease (Seidl et al. 2011), are considered.

Although it may be difficult to predict future fire regimes accurately for a given location, the differences between simulations run under a range of conditions will inform management decisions (Keane et al. 2004). For example, when given a range of possible outcomes, managers can weigh the relative need for prescribed burning, firefighting, and buffering of wildlife habitats. Empirical models have illustrated relationships between 20th century climate and area burned (Littell et al. 2009) and fire frequency (Gedalof et al. 2005), suggesting increased fire risk given projected future climate. Process-based fire simulation models suggest that negative feedback from forest clearing and previous fires may reduce, but not eliminate, projected climate-induced increases in area burned (Krawchuck and Cumming 2010). These models, along with near- and long-term climate projections, may help to identify where adaptive management techniques might be cost-effective and how much fire-control costs may escalate (Corringham et al. 2008). Reliable climate forecasts a season or two in advance could inform national fire management plans in time for proactive management. Long-term projections of climate can be used to assess potential impacts of climate-altered fire regimes on vegetation.

Case study. Wildfire impacts nutrient cycles, young trees and understory vegetation, and the distribution of water and sediment, all of which can impact fish and wildlife habitats (Noss et al. 2006). Changes in wildfire may benefit some wildlife species at the expense of others (e.g., Smucker et al. 2005), making it critical to characterize the direction and magnitude of projected change. Annual area burned, fire season length, and the frequency of large fires have been used to characterize regional changes in wildfire (Westerling et al. 2006) and can be estimated from GCM outputs (e.g., Westerling and Bryant 2007). Identifying regions with increasing risk of fire under climate change would alert managers to the need for planning and treatment to protect critical

Box 3
Future area burned in Canada
(Flannigan et al. 2005)

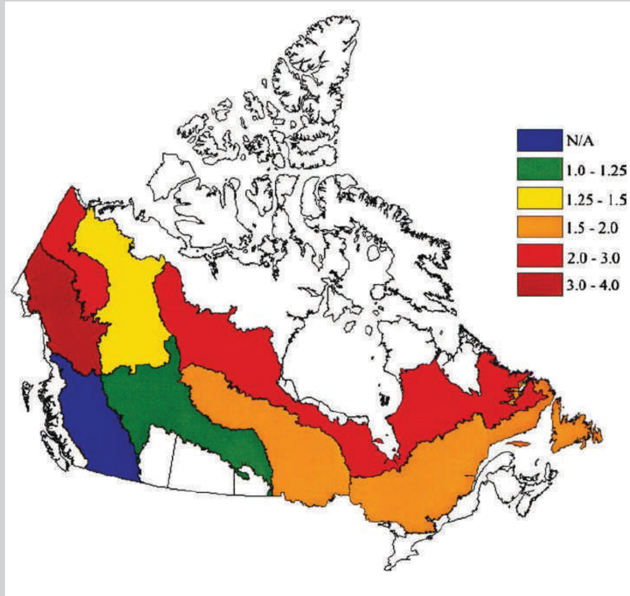

Figure 3-1. *Ratio of 3 × CO_2 : 1 × CO_2 area burned by ecozone using a a single general circulation model. N/A, not applicable; the area burned model did not work for this ecozone. Adapted from Flannigan et al. (2005) with kind permission from Springer Science and Business Media.*

Phase I: Project Scoping

Changes in the extent of wildfire may impact the composition and structure of vegetation across regions, impacting wildlife habitat availability. Flannigan et al. estimated how the tripling of atmospheric CO_2 projected for the end of the century would impact the annual forest area burned in eight ecozones across Canada. They assumed that annual area burned across each ecozone is a function of weather and assembled historical meteorological data and fire records to look for those relationships.

Phase II: Modeling

Flannigan et al. built empirical linear regression models that used historical measures of fuel-moisture content, build up, potential spread, and a composite measure—the Canadian forest fire weather index—derived from meteorological data as predictors of area burned. They then predicted area burned from simulated climate output from two general circulation models under a 3 × CO_2 scenario.

Phase III: Summary and Interpretation

The ratio of future to current estimated area burned was presented as a metric of potential change. Models project from 0–3.81 times more annual area burned among ecozones with projections from one model nearly 50% greater (Figure 3-1). Areas of greatest impact include the boreal forest and taiga ecozones. These results suggest that area burned could rise from current levels, ~1.8 million ha, to 3–4 million ha by the end of the century potentially facilitating broad-scale changes in vegetation and wildlife habitats as well as increasing fire management costs.

wildlife areas as well as to potentially looming suppression costs.

Flannigan et al. (2005) used statistical models to predict annual forest area burned across Canada under simulated future climates (Box 3). Models were constructed for eight ecozones reflecting broad-scale historical differences in fire frequency and extent. Models used historical meteorological data as predictors of area burned calculated from a large fire database spanning 1959–1997 (Stocks et al. 2002). Projections were made using outputs from two GCM models run for a single emissions scenario that simulated a tripling of atmospheric CO_2 concentrations by the end of the century. Outputs suggest that annual area burned by wildfires will likely increase across Canada. There is some uncertainty among the GCM models used regarding the magnitude of the increase, but no ecozones were projected to experience declining wildfire. The potential addition of millions of hectares burned annually could result in dramatic changes in the distribution of vegetation and associated wildlife across Canada. These results are most informative for improving regional forest management policy, but they are too coarse in resolution for assessing the impacts at a specific location. Furthermore, outputs from a larger number of GCMs would better characterize the uncertainty surrounding the magnitude of projected increases. In spite of their limitations, these results suggest that evaluating fire impacts on fish and wildlife habitats across the boreal forest and taiga regions of Canada would be useful to identify wildlife species that may require protection or assistance under increasing wildfire.

Vegetation models

Vegetation is fundamental for terrestrial food webs and is an essential element in the habitat of many animal species. As climates change, plant species ranges will shift; biomes will exhibit altered characteristics; and the structure and composition of vegetation communities will adjust, all influencing habitat and food resources for many animals. Therefore, vegetation models have the potential to provide insight for local- to continental-scale management, policy and for planning decisions regarding wildlife.

Vegetation models range from statistical models that identify relationships between plant distributions and environmental variables to mechanistic models that simulate the physical processes controlling the distribution of vegetation. Statistical models are often used to project changes in the distributions of individual plant species or communities (e.g., Rehfeldt et al. 2012). These models are described in the Individual Species Models section below. Here, we focus on process-based vegetation models.

Process-based vegetation models simulate aspects of plant physiology (e.g., photosynthesis), carbon and nutrient cycles, competition between individual plants or vegetation types, disturbance regimes, hydrology, and other processes. They include forest gap models (e.g., Bugmann 2001; Larocque et al. 2011), landscape models (e.g., Keane et al. 2004; Keane et al. 2011), terrestrial biogeochemistry models of carbon and nutrient cycles (e.g., Parton et al. 2007), dynamic global vegetation models (Cramer et al. 2001; Quillet et al. 2010), and coupled hydrology–vegetation models (e.g., Tague and Band 2004; Lawrence et al. 2011). Vegetation in these models is represented as individual species, plant functional types (e.g., deciduous broadleaf trees and grass), or by using general measures of vegetation (e.g., net primary productivity). The models may simulate processes on subdaily to annual time-steps and over spatial extents ranging from individual plot to global. Input data for these models typically include climate data (e.g., temperature and precipitation), atmospheric CO_2 concentrations, and soil characteristics (e.g., soil texture). The models may specify bioclimatic limits (e.g., lethal temperatures) and other biophysical parameters (e.g., rooting depth and fire resistance) for particular species or vegetation types. Dynamic vegetation models can simulate changes in vegetation over time in response to changing climate, whereas equilibrium vegetation models simulate vegetation under a static climate (e.g., average conditions).

Limitations and uses. The ecological processes simulated in vegetation models are complex. In many cases, the calculations of particular processes may require empirical parameters that are not well known. For example, changes in atmospheric CO_2 concentrations can affect plant water-use efficiency, but more information about how this effect varies among different plant species and life stages is needed to better represent this response in vegetation models. Furthermore, individual vegetation models may explicitly simulate some processes, such as fire, but either ignore or simplify other processes, such as grazing and insect outbreaks, that may be as important in determining the distribution of vegetation in certain areas (Seidl et al. 2011). As one might expect, the assumptions made in the building and parameterization of vegetation models can substantially affect model projections (Cramer et al. 2001; Quillet et al. 2010).

Vegetation models vary in their complexity and ease of use. Applying these models to particular management and research questions can require a detailed understanding of ecosystem processes and computer programming expertise to correctly parameterize a model. Vegetation models also differ in their ability to account for the effects of land-use practices and land-cover changes that may alter the flow of water or nutrients, fire regimes, or the vegetation itself. To more accurately project future climate-driven vegetation changes, future vegetation models will need to incorporate land-use projections and simulate their effects on vegetation.

Despite their limitations, all of the types of process-based vegetation models discussed above have been applied to conservation and natural resource management questions, including silvicultural applications (Pabst et al. 2008), forecasting areas of potential fire risk (Lenihan et al. 2008), and simulating future changes in habitat (Morin and Thuiller 2009). The choice of which model or combination of models to apply to a particular management question will depend on the specific aspects of vegetation one wishes to simulate; its spatial and temporal resolution; and the importance of particular processes, such as fire. For example, forest gap models simulate stand-level processes, but many are limited in their ability to predict vegetation responses across broader spatial scales (Bugmann 2001). In contrast, a dynamic global vegetation model may simulate basic plant functional types that can be translated into vegetation types or biomes (e.g., broadleaf evergreen forest, grassland, and conifer woodland) over regional to global scales, but it may not be able to simulate gradients in species composition or forest stand structure.

Some limitations can be overcome by integrating models of varying complexity and scale. For example, aspects of forest gap models have been incorporated into both landscape models (e.g., He et al. 2005; Keane et al. 2011) and dynamic vegetation models (e.g., Smith et al. 2001) to improve their simulations of plot-level vegetation dynamics. Another approach uses a mathematical approximation to scale-up the outcome of stochastic gap model processes to resolutions suitable for subcontinental scales (Moorcroft et al. 2001), resulting in output that is both locally accurate and transferable across regions (Medvigy et al. 2009). Although vegetation models generally cannot predict future vegetation changes with high accuracy and spatial resolution, the models can help managers to characterize the future rates and magnitudes of potential vegetation changes and to identify species and regions that may be particularly sensitive (or particularly resilient) to future climate changes (e.g., Lenihan et al. 2008). These results in turn can be used to help inform the management of animal species and their habitat in the face of climate change. They can provide guidance on where to restore and where not to restore habitats, which populations to monitor, and where populations will need to be intensively managed.

Case study. Prairies and savannahs are some of the most threatened ecosystems in the United States (Hoekstra et al. 2005). Consequently, the prairies and savannas of the Pacific Northwest are home to a large number of state-listed and federal candidate species, including the streaked horned lark *Eremophila alpestris strigata*, Taylor's checkerspot butterfly *Euphydras editha taylori*, Mazama pocket gopher *Thomomys mazama*, and western gray squirrel *Sciurus griseus*. Managing populations of these species requires an understanding of how climate change will alter their habitats. Projected changes in vegetation across the Pacific Northwest will have the potential to inform decisions about which populations to monitor, where to put limited restoration dollars, and how to plan for connectivity. Bachelet et al. (2011) summarized output from a dynamic global vegetation model (Rogers et al. 2011) projecting potential climate-driven changes in vegetation in the Willamette Valley-Puget Trough-Georgia Basin ecoregion (Box 4). From all of the GCMs in the IPCC AR4, they selected three GCMs whose projections captured the range of outputs for the region and included three CO_2 emissions scenarios. Of the nine model runs considered, none projected an increase in prairie and savanna habitats for the end of the century, likely because the dynamic global vegetation model simulated higher water use efficiency in trees accompanying greater atmospheric CO_2 concentrations, thereby increasing their tolerance of drought. Instead, the cool and wet climate projection produced no change in simulated vegetation distributions, the hot and dry projection simulated the western expansion of dry forest from the eastern Cascades, and the hot and wet projection simulated the northward expansion of warmer forests. Thus, prairie and savanna ecosystems appear likely to remain rare with climate change. Yet, empirical evidence assembled by Bachelet et al. (2011) suggests that prairies and savannas may be more resilient than forests to warm and dry summers, particularly if climate change brings more extreme drought and fire. Bachelet et al. (2011) therefore advise managers to restore prairies in unproductive agricultural lands and forest lands that are likely to become warmer and drier with climate change. Managers also may want to consider assisted migration within the ecoregion to increase populations of rare species. Finally, managers may want to monitor and improve existing sites that are likely to continue functioning as prairies over the coming century.

Individual species models

The ultimate goal of fish and wildlife management is stable, resilient animal populations that can only be assessed with species-specific models. Individual species models can be designed to estimate habitat suitability, species distributions, movement, and population-level (i.e., demographic) responses. Many modeling approaches that estimate historical changes in populations of threatened and endangered species also can be used to simulate future climate-induced changes.

Empirical approaches, typically referred to as climate-envelope, niche, or bioclimatic models, are used to project potential climate-driven shifts in species distributions (Pearson and Dawson 2003; Heikkenen et al. 2006). These models use either statistical or machine-learning methods to identify relationships between current species distributions and current climate, and they use future climate to generate projected distributions. Most empirical models use only climatic variables as predictors (e.g., temperature, precipitation, growing degree days, and drought indices), but some have incorporated other variables, such as land cover, elevation, or soil type (Prasad et al. 2006).

Whereas empirical models have generally been used to project changes in species' potential distributions, process-based models have been used to simulate a wider array of species-specific ecological effects. For example, dispersal models can simulate movement in response to climate change (e.g., Iverson et al. 2004); population models can simulate annual recruitment as a function of climate-driven changes in habitat, food resources, predators, or competitors (e.g., Carroll 2007); distribution models can make projections based on phenology, reproduction, and survival (e.g., Morin and Thuiller 2009); and bioenergetic models can project the responses of trophic groups (e.g., phyto- and zooplankton) to climate-driven changes in total energy (e.g., Peeters et al. 2007). Generally, climate is incorporated into these models through empirical relationships between temperature, precipitation, or both and individual fitness, such as making growth and reproduction a function of water temperature (Clark et al. 2003) or varying survival with annual snowfall (Carroll 2007). Empirical and process-based models also can be linked; for example, using empirical models of habitat suitability as input to a process-based population model (e.g., Carroll 2007; McRae et al. 2008; Franklin 2010; Lawson et al. 2010).

Limitations and uses. Empirical species distribution models provide a preliminary estimate of how plant and animal distributions may respond to climate change, but they have several limitations. First, empirical models do not directly model biotic interactions (e.g., predator–prey dynamics, keystone species, competition, or host specificity) that may influence potential range shifts (Pearson and Dawson 2003; Zarnetske et al. 2012). Second, these models generally do not address dispersal capacity or barriers to dispersal that may influence colonization of projected habitats (Pearson and Dawson 2003; Schloss et al. 2012). Third, empirical models do not consider evolutionary adaptation (Pearson and Dawson 2003). Fourth, it is unclear how models parameterized under present-day climates will perform in simulated future climate with no present-day analog (Williams and Jackson 2007; Williams et al., 2013). Fifth, bioclimatic tolerances may vary across life stages, impacting persistence and colonization (Jackson et al. 2009; Mclaughlin and Zavaleta 2012). Sixth, different types of empirical models can produce very different projected shifts in the potential range of a species, sometimes introducing more uncertainty than the underlying GCM projections (Garcia et al. 2012), necessitating care in model selection and testing (Thuiller 2004) or using ensembles of multiple models (Araújo and New 2007).

Given these limitations, empirical species distribution models are not currently accurate enough to be the sole source of information for selecting reserve networks,

Box 4
Climate change impacts on western Pacific Northwest prairies and savannas
(Bachelet et al. 2011)

Phase I: Project Scoping

Many threatened and endangered wildlife species are associated with rare vegetation types, such as prairies and savannas. Bachelet et al. examine projected end-of-century change in vegetation cover in the Willamette Valley-Puget Trough-Georgia Basin ecoregion to assess the persistence of remnant prairies and savannas. Their vegetation simulations are available for open-access on the Data Basin (databasin.org) website.

Phase II: Modeling

Bachelet et al. use vegetation projections from the MC1 dynamic global vegetation simulation model (Rogers et al. 2011) run with output from three general circulation models (CSIRO[1], Hadley[2], and MIROC[3]) under under low, medium and high CO_2 emissions scenarios (B1, A1B, A2, respectively, Figure 4-1).

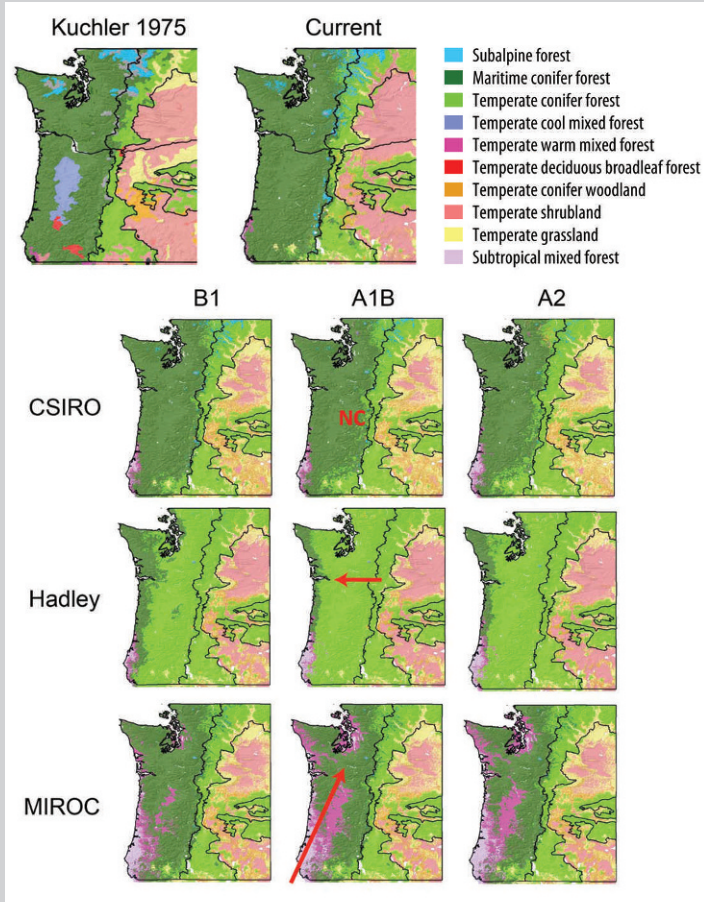

Figure 4-1. *Vegetation projections from the MC1 dynamic global vegetation simulation model (Rogers et al. 2011) run with output from three general circulation models (CSIRO[1], Hadley[2], and MIROC[3]) under low, medium, and high CO_2 emissions scenarios (B1, A1B, A2, respectively). Adapted from Bachelet et al. (2011).*

Phase III: Summary and Interpretation

The end-of-century distributions of simulated vegetation types varied considerably among general circulation models, but less so among emissions scenarios. Outcomes of no change in vegetation cover (NC), western expansion of dry forest conifers from the eastern Cascades and northward expansion of warm-adapted mixed forests (highlighted with arrows) were all simulated; whereas no models or scenarios simulated an increase in prairie or savanna habitats. Thus, prairies and savannas are likely to remain rare under a changing climate and the authors recommend active restoration of remaining and potential sites as well as translocation of prairie- and savanna-dependent wildlife species to unoccupied sites.

[1] Commonwealth Scientific and Industrial Research Organisation model, CSIRO Mk3.0 (Australia)
[2] Hadley Centre coupled model, HadCM3 (UK)
[3] Center for Climate Systems Research Model for Interdisciplinary Research on Climate, MIROC 3.2 medres (Japan)

identifying translocation sites, or deciding to abandon management of a population. However, they are likely to be useful for identifying populations at risk due to a significant climate-driven range contraction (Pearson and Dawson 2003). These models also can help focus conservation efforts and monitoring programs by identifying habitats where we might expect to see the largest changes in flora or fauna (Araújo et al. 2006). For specific management decisions regarding individual species, these models can be used in conjunction with experimental information, paleoecological records, and simulations from detailed process-based models to increase projection accuracy.

Although process-based models of species distributions and populations have the potential to provide more accurate projections than empirical models, they also have limitations. Many of these limitations are similar to those discussed above in reference to the vegetation models. First, many of the parameters and relationships that would ideally be incorporated into these models are poorly known, such as dispersal rates and temperature and precipitation effects on survival and reproduction. Second, the structure of process-based models may limit their application. Some are built to investigate the effect of one particular aspect of climate (e.g., temperature) on reproduction, growth, or survival (Kell et al. 2005) and may exclude other critical factors (e.g., dispersal, Clark et al. 2003). Still, when sufficient empirical information is available to parameterize a process-based model, the model is useful for characterizing population-level responses to climate change. Furthermore, process-based models linked with other empirical (e.g., habitat) or process-based models (e.g., vegetation, hydrology, and fire) can be used to simulate cumulative effects (Lawson et al. 2010) or to compare the relative effects of stressors (Battin et al. 2007; Carroll 2007; McRae et al. 2008) on species' populations.

Case study. Marten and lynx *Lynx canadensis* in the northern Appalachians of the United States and Canada forage on top of snowpack during the winter, making them sensitive to rising temperatures and declining snowfall. Both are exploited populations occurring at the southern limit of their distributions. Marten, in particular, has recovered from near extirpation in the 1930s. Marten populations are also sensitive to the loss and fragmentation of mature forest stands with structurally complex understories (Ray 2000). In an approach similar to that taken by Battin et al. (2007), Carroll (2007) linked multiple models to estimate the relative impacts of climate change, logging, and hunting on marten populations in the northern Appalachians (Box 5). The system of linked models allowed for scenarios addressing stressors individually and in combination. Simulations demonstrated that declining snowpack may have a greater impact than logging or trapping alone and that logging may interact synergistically with climate change to decrease marten populations. Carroll (2007) summarizes results by state and province and makes region-specific recommendations for habitat restoration, logging, exploitation, and reintroduction potential. These types of outputs would be very useful for species and habitat management as well as decisions on logging and hunting. However, the use of a single GCM and single emissions scenario puts into question the generality of these findings. Carroll (2007) does note that there is agreement among all IPCC AR4 GCMs regarding the direction and magnitude of projected changes in temperature and precipitation for this geographic region. However, representing that variability explicitly would strengthen his conclusions.

Discussion

Using models for managing natural resources

Given the wide array of available models and their numerous limitations (Table 1), fish and wildlife managers often wonder which model to use and how to apply model projections to a given management decision. We have provided a basic framework for climate-impacts modeling (Box 1) and used it to discuss the results of several climate-impact studies (Boxes 2–5). In general, selecting one or more models to assess potential climate impacts requires an understanding of the underlying question and the key ecological processes involved. For example, modeling climate impacts on fire-dependent wildlife habitats will require, at the minimum, a vegetation model that adequately addresses the effects of climate on fire. Selecting an appropriate model also requires matching the spatial and temporal scale of the assessment with that of the model. For example, although a macroscale hydrological model may provide a useful estimate of runoff for a watershed, it may provide relatively poor estimates of changes in stream flow for a specific stream reach. The selection of a particular model also will depend on the time, resources, and technical capabilities available to the user. Here, the difference between empirical and statistical models and simulation models is paramount. Empirical models are less complex, require fewer inputs, and are generally more accessible; but they include a suite of biological assumptions that observational data suggest are violated. Therefore, they are most appropriate for coarse-scale projections of climate responses. A complex simulation model may provide the best estimate of a species' response to climate change, but often data, time, modeling expertise, or a combination are lacking. In those cases, first consider whether a broad-scale modeling analysis including the geographic area of interest has already been completed. Alternatively, rethink the management question to no longer require the additional accuracy (or ecological realism) that might be provided by a more complex model, for example, choosing to focus on changes in habitat suitability instead of population demographics.

Increasingly, downscaled climate projections are available online (e.g., ClimateWizard, http://www.climatewizard.org and the Oregon Climate Change Research Institute, http://occri.net), and projections from hydrological, fire, and vegetation models are being shared through cooperative associations such as the U.S. Department of Interior's Landscape Conservation Cooperatives (http://www.doi.gov/lcc/index.cfm), the U.S. Geological Survey's National Climate Change and Wildlife Science Center (https://nccwsc.usgs.gov), and nongovernmental data-sharing portals such as Data Basin (http://www.databasin.org). As these datasets become more ubiquitous, it is critical for nonspecialists to understand appropriate uses for model outputs.

Understanding the thornier issue of how model results can inform management is as important as selecting the best set of models for an assessment. No model can predict the future with certainty. Furthermore, the uncertainties inherent in future climate-change projections are increased when linked to ecological climate-impacts models that have their own associated uncertainty (Maslin and Austin 2012). In the case studies described above, both Battin et al. (2007) and Carroll (2007) linked multiple models to explore climate impacts in conjunction with other stressors. Similar studies have been completed for songbirds (McCrae et al. 2008), wolverine (McKelvey et al. 2011), and plants (Lawson et al. 2010). The best applications of these models treat uncertainty explicitly. Thorough sensitivity analyses calculating the impact of varying all components in a system of linked models are currently rare (but see Fuller et al. 2008; Conlisk et al. 2013), but they should be pursued when possible to better understand the behavior of any complex model. Evaluating projections

Box 5

Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the Northern Appalachians (Carroll 2007)

Phase I: Project Scoping

Climate change is likely to have both direct (e.g., physiological) and indirect (through changing habitats and resources) impacts on individual fish and wildlife species and these may compound or offset existing threats. Individual species simulation models can be used to quantify the cumulative impacts of multiple interacting stressors. Carroll explored how simulated climate change, expansion of logging, and continued hunting would affect marten (*Martes americana*) populations in the Northern Appalachians through 2055. He assembled marten harvest data and empirical demographic data to use in building habitat suitability and population models. Carroll assumed that declining snowpack and logging decrease habitat availability, and that harvest decreases survival.

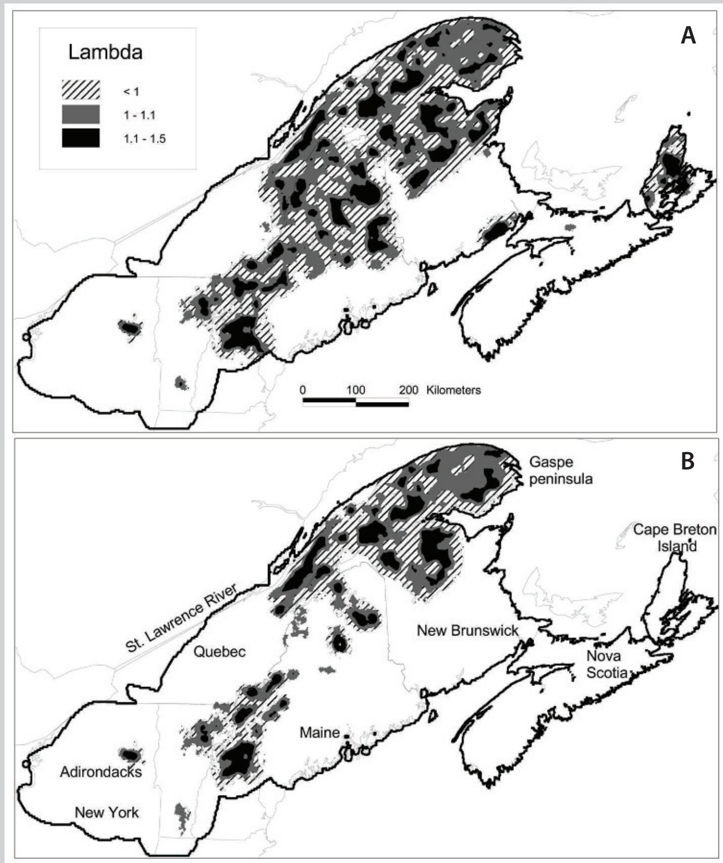

Figure 5-1. *Marten distribution in the Northern Appalachians. Projected population growth rates (lambda) for marten in the northern Appalachians (USA and Canada) under current (A) and projected (B) snowfall levels based on projections from a spatially explicit population model (PATCH, Schumaker et al. 2004). Adapted from Carroll (2007), © 2007 Society for Conservation Biology.*

Phase II: Modeling

Carroll modeled habitat suitability with a statistical model in which forest cover and snowpack were predictor variables. He then mapped future habitat with output from a general circulation model run under a single CO_2 emissions scenario. Finally, he simulated marten populations with a spatially explicit individual based population model (PATCH, Schumaker et al. 2004, renamed HexSim in 2011). The population model also incorporated year-to-year variability in fecundity and survival due to alternate-year mast cycles. Increased logging was simulated by a 10% reduction in forest cover and trapping was simulated with a 10% decline in survival.

Phase III: Summary and Interpretation

Carroll produced yr-2055 population estimates and maps of the simulated population growth rate (lambda) for comparisons among scenarios. Climate-induced changes in snowpack were projected to cause local extirpation of isolated marten populations as well as those currently found in lowland areas (Figure 5-1). Carroll's simulations indicated that projected declines in snowpack may have a greater impact on populations than trapping or logging alone. Furthermore, climate impacts and habitat loss from logging interacted synergistically to decrease marten populations. These results suggest that the Appalachian marten population is severely threatened by climate change and that this threat may be exacerbated by logging.

from multiple GCMs and emissions scenarios is also critical for quantifying uncertainty. For example, studies indicate that using an ensemble of GCM projections, preferably more than 10, is more important than the careful selection of one or two projections for characterizing future hydrologic impacts of climate change (Pierce et al. 2009). Such approaches bracket potential future outcomes of climate change and can be used in making consensus recommendations for conservation or in designing management actions robust to a range of climate impacts (e.g., Bachelet et al. 2011).

Ensemble modeling combines the outputs of multiple model projections, allowing the modeler to quantify the confidence in model outputs across an array of different inputs or model structures (Araújo and New 2007). For example, ensembles of models can project mean or median warming with associated confidence bands (Solomon et al. 2007). Alternatively, ensembles can be used to report the degree of agreement in model projection; for example, 80% of modeled future climates project at least a 50% change in the fauna of a given region (Lawler et al. 2009). Although depicting only mean values or the degree of consensus among model projections can be useful, it also can be misleading. Agreement within a set of model projections does not mean that those models are correct. In some cases, such as projecting the severity of future drought or flood events, projections of extremes (minimums or maximums) may be more critical than consensus or mean projections (e.g., Deser et al. 2012). However, agreement among models with different structures does suggest that those projections are robust to the assumptions of multiple model designs (Morin and Thuiller 2009), implying that the projections reflect a true underlying pattern or trend.

Scenario-based modeling provides another approach to exploring the potential effects of varying model inputs or parameterizations. A scenario is a set of model inputs reflecting how a system may behave or change. Examples of scenarios include differing CO_2 emissions rates, patterns of urban development, and estimates of plant water-use efficiency responses. Scenario-based modeling contributes to the process of scenario-based planning in which decisions are made by exploring the impacts of several different potential future outcomes (Peterson et al. 2003). Scenario-based modeling can be used to compare the effects of particular climatic changes (e.g., warmer and wetter vs. warmer and drier climates) or to compare the potential effects of extreme and mean projected changes. The IPCC, among others, has provided guidance on scenario-based planning in the context of climate change (IPCC-TGICA 2007).

Climate change vulnerability assessment provides a framework for integrating climate-impacts projections with empirical information to characterize the vulnerability of species or ecological systems to climate change (Williams et al. 2008; Glick et al. 2011). Vulnerability depends on a species' exposure and sensitivity to climate change as well as its adaptive capacity and therefore integrates information from diverse sources, including modeling, natural history, experimental science, and paleoecological records (Dawson et al. 2011; and, e.g., http://climatechangesensitivity.org). Vulnerability scores and rankings can then point toward additional studies or information gaps that help integrate climate change into natural resource management decisions.

Another, complementary, way to use uncertain information in the decision-making and planning process is through adaptive management (Holling 1978; Peterson et al. 2011). Adaptive management is an iterative process in which multiple management actions are evaluated with long-term monitoring, the outcome of which is used to inform future management (Figure 1). The inherent uncertainty of the ecological impacts of climate change makes it an appropriate application of an adaptive management framework (Arvai et al. 2006). Outputs of climate-impacts models can be used to design a suite of short-term management prescriptions and then be recalibrated with data or knowledge gained from their monitoring. In one example, a hydrological model will be used within an adaptive management framework to reduce the frequency of algal blooms under future climates (Viney et al. 2007). Adaptive management will likely be a key tool for dealing with the uncertainties inherent in climate-impacts projections (West et al. 2009; Littell et al. 2011).

Conclusions

Climate-impacts modeling is a rapidly expanding field of research. Models are becoming more sophisticated and better able to capture physical and ecological processes. Yet, at best, models will be an approximation of an uncertain future. Therefore, it will always be critical to address model uncertainty through model ensembles and a range of future scenarios and to reevaluate decisions regularly, ideally in a framework of adaptive management. Also of value are ways of integrating model outputs with experimental results, paleoecological records (e.g., Martínez-Meyer et al. 2004), and expert opinion. Questions to ask of any climate-impacts study include the following: How well do you capture the range of potential futures? How much agreement is there among those models and scenarios? Can you develop management strategies that are resilient to all potential futures? This last question points toward climate change adaptation for which many institutional frameworks exist (Bachelet et al. 2010) and toward which climate-impacts modeling can contribute.

Models play a critical role in our understanding of climate-change impacts on ecological systems. For these models to be useful, the uncertainties in model projections need to be understood. However, these uncertainties should not prevent researchers and managers from using models to explore potential future climate impacts, assess vulnerabilities, and develop adaptation strategies.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Reference S1. Andrews P, Bevins C, Seli R. 2004. BehavePlus Fire Modeling System, version 3.0: user's guide. Ogden, Utah: USDA Forest Service. General Technical Report RMRS-GTR-106.

Found at DOI: http://dx.doi.org/10.3996/062012-JFWM-055.S1; also available at http://www.firelab.org/science-applications/science-synthesis/69-behaveplus (5.7 MB PDF).

Reference S2. Keane RE, Loehman RA, Holsinger LM. 2011. The FireBGCv2 landscape fire and succession model: a research simulation platform for exploring fire and vegetation dynamics. Fort Collins, Colorado: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. General Technical Report RMRS-GTR-255.

Found at DOI: http://dx.doi.org/10.3996/062012-JFWM-055.S2; also available at http://www.firelab.org/research-projects/fire-ecology/139-firebgc (3.4 MB PDF).

Reference S3. Peterson DL, Millar CI, Joyce LA, Furniss MJ, Halofsky JE, Neilson RP, Morelli T-L. 2011. Responding to climate change in national forests: a guidebook for developing adaptation options. Portland, Oregon: Pacific Northwest Research Station. USDA Forest Service. General Technical Report PNW-GTR-855.

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References

Andrews P, Bevins C, Seli R. 2004. BehavePlus Fire Modeling System, version 3.0: user's guide. Ogden, Utah: USDA Forest Service. General Technical Report RMRS-GTR-106 (see *Supplemental Material*, Reference S1, http://dx.doi.org/10.3996/062012-JFWM-055.S1); also available: http://www.firelab.org/science-applications/science-synthesis/69-behaveplus (March 2013).

Araújo MB, New M. 2007. Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22:42–47.

Araújo MB, Thuiller W, Pearson RG. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712–1728.

Arvai J, Bridge G, Dolsak N, Franzese R, Koontz T, Luginbuhl A, Robbins P, Richards K, Smith Korfmacher K, Sohngen B, Tansey K, Thompson A. 2006. Adaptive management of the global climate problem: bridging the gap between climate research and climate policy. Climatic Change 78:217–225.

Bachelet D, Brooks ML, Cross MS, Enquist CAF, Fleishman E, Graumlich L, Groves CR, Hannah L, Hansen L, Hayward G, Koopman M, Lawler JJ, Malcolm J, Nordgren J, Petersen B, Scott D, Shafer SL, Shaw MR, Tabor GM, Zavaleta ES. 2010. Climate Change Adaptation for Conservation Targets (ACT) Framework. Available: http://www.cakex.org/virtual-library/2285 (January 2013).

Bachelet D, Johnson BR, Bridgham SD, Dunn PV, Anderson HE, Rogers BM. 2011. Climate change impacts on western Pacific Northwest prairies and savannas. Northwest Science 85:411–429.

Battin J, Wiley MW, Ruckelshaus MH, Palmer RN, Korb E, Bartz KK, Imaki H. 2007. Projected impacts of climate change on salmon habitat restoration. Proceedings of the National Academy of Sciences of the United States of America 104:6720–6725.

Bernhardt ES, Palmer MA, Allan JD, Alexander G, Barnas K, Brooks S, Carr J, Clayton S, Dahm C, Follstad-Shah J, Galat D, Gloss S, Goodwin P, Hart D, Hassett B, Jenkinson R, Katz S, Kondolf GM, Lake PS, Lave R, Meyer JL, O'Donnell TK, Pagano L, Powell B, Sudduth E. 2005. Synthesizing U.S. river restoration efforts. Science 308:636–637.

Betts RA, Boucher O, Collins M, Cox PM, Falloon PD, Gedney N, Hemming DL, Huntingford C, Jones CD, Sexton DMH, Webb MJ. 2007. Projected increase in continental runoff due to plant responses to increasing carbon dioxide. Nature 448:1037–1041.

Bony S, Colman R, Kattsov VM, Allan RP, Bretherton CS, Dufresne JL, Hall A, Hallegatte S, Holland MM, Ingram W, Randall DA, Soden BJ, Tselioudis G, Webb MJ. 2006. How well do we understand and evaluate climate change feedback processes? Journal of Climate 19: 3445–3482.

Botkin DB, Saxe H, Araújo MB, Betts R, Richard HWB, Cedhagen T, Chesson P, Dawson TP, Etterson JR, Faith DP, Ferrier S, Guisan A, Hansen AS, Hilbert DW, Loehle C, Margules C, New M, Sobel MJ, Stockwell DRB. 2007. Forecasting the effects of global warming on biodiversity. Bioscience 57:227–236.

Brekke LD, Dettinger MD, Maurer EP, Anderson M. 2008. Significance of model credibility in estimating climate projection distributions for regional hydroclimatological risk assessments. Climatic Change 89:371–394.

Bugmann H. 2001. A review of forest gap models. Climatic Change 51:259–305.

Carroll C. 2007. Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the Northern Appalachians. Conservation Biology 21:1092–1104.

Cherkauer KA, Lettenmaier DP. 2003. Simulation of spatial variability in snow and frozen soil. Journal of Geophysical Research-Atmospheres 108:8858.

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon W-T, Laprise R, Magaña Rueda V, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P. 2007. Regional climate projections. Pages 848–940 in Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, editors. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate. Cambridge, UK: Cambridge University Press. Available: http://www.ipcc.ch/publications_and_data/ar4/wg1/en/contents.html (April 2013).

Clark RA, Fox CJ, Viner D, Livermore M. 2003. North Sea cod and climate change – modeling the effects of temperature on population dynamics. Global Change Biology 9:1669–1680.

[CMIP] Coupled Model Intercomparison Project. 2010. Coupled Model Intercomparison Project. Available: http//:cmip-pcmdi.llnl.gov (June 2010).

Conlisk E, Syphard A, Franklin J, Flint L, Flint A, Reagan H. 2013. Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. Global Change Biology 19:858–869.

Corringham TW, Westerling AL, Morehouse BJ. 2008. Exploring use of climate information in wildland fire management: a decision calendar study. Journal of Forestry 106:71–77.

Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling CY. 2001. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Global Change Biology 7:357–373.

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58.

Deser C, Phillips A, Bourdette V, Teng H. 2012. Uncertainty in climate change projections: the role of internal variability. Climate Dynamics 38:527–546.

Doten CO, Bowling LC, Lanini JS, Maurer EP, Lettenmaier DP. 2006. A spatially distributed model for the dynamic prediction of sediment erosion and transport in mountainous forested watersheds. Water Resources Research 42:W04417.

Ficklin DL, Luo Y, Stewart IT, Maurer EP. 2012. Development and application of a hydroclimatological stream temperature model within the Soil and Water Assessment Tool. Water Resources Research 48: W01511.

Flannigan MD, Krawchuk MA, de Groot WJ, Wotton BM, Gowman LM. 2009. Implications of changing climate for global wildland fire. International Journal of Wildland Fire 18:483–507.

Flannigan MD, Logan KA, Amiro BD, Skinner WR, Stocks BJ. 2005. Future area burned in Canada. Climatic Change 72:1–16.

Fowler HJ, Blenkinsop S, Tebaldi C. 2007. Linking climate change modelling to impacts studies: recent advances in downscaling techniques for hydrological modelling. International Journal of Climatology 27:1547–1578.

Franklin J. 2010. Moving beyond static species distribution models in support of conservation biogeography. Diversity and Distributions 16:321–330.

Fuller T, Morton DP, Sarkar S. 2008. Incorporating uncertainty about species' potential distributions under climate change into the selection of conservation areas with a case study from the Arctic Coast Plain of Alaska. Biological Conservation 141:1547–1559.

Garcia RA, Burgess ND, Cabeza M, Rahbek C, Araújo MB. 2012. Exploring consensus in 21st century projections of climatically suitable areas for African vertebrates. Global Change Biology 18:1253–1269.

Gedalof Z, Peterson DL, Mantua NJ. 2005. Atmospheric, climatic, and ecological controls on extreme wildfire years in the northwestern United States. Ecological Applications 15:154–174.

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.

Glick P, Stein BA, Edelson NA. 2011. Scanning the conservation horizon: a guide to climate change vulnerability assessment. Washington, D.C.: National Wildlife Federation.

Graham LP, Hagemann S, Jaun S, Beniston M. 2007. On interpreting hydrological change from regional climate models. Climatic Change 81:97–122.

Guilyardi E, Bellenger H, Collins M, Ferrett S, Cai W, Wittenberg AT. 2012. A first look at ENSO in CMIP5. CLIVAR Exchanges 58:29–32.

Haddeland I, Skaugen T, Lettenmaier DP. 2007. Hydrologic effects of land and water management in North America and Asia: 1700–1992. Hydrology and Earth System Sciences 11:1035–1045.

Harsch MA, Hulme PE, McGlone MS, Duncan RP. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Hartmann DL. 1994. Global physical climatology. San Diego, California: Academic Press.

Hawkins E, Sutton R. 2009. The potential to narrow uncertainty in regional climate predictions. Bulletin of the American Meteorological Society 90:1095–1107.

Hawkins E, Sutton R. 2011. The potential to narrow uncertainty in projections of regional precipitation change. Climate Dynamics 37:407–418.

He HS, Hao Z, Mladenoff DJ, Shao G, Hu Y, Chang Y. 2005. Simulating forest ecosystem response to climate warming incorporating spatial effects in northeastern China. Journal of Biogeography 32:2043–2056.

Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30:751–777.

Higuera PE, Brubaker LB, Anderson PM, Hu FS, Brown TA. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecological Monographs 79:201–219.

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Holling CS. 1978. Adaptive environmental assessment and management. New York: Wiley.

[IPCC-TGICA] Intergovernmental Panel on Climate Change Task Group on Data and Scenario Support for Impact and Climate Assessment. 2007. General guidelines on the use of scenario data for climate impact and adaptation assessment, version 2. Carter TR (lead author), Alfsen K, Barrow E, Bass B, Dai X, Desanker P, Gaffin SR, Giorgi F, Hulme M, Lal M, Mata LJ, Mearns LO, Mitchell JFB, Morita T, Moss R, Murdiyarso D, Pabon-Caicedo JD, Palutikof J, Parry ML, Rosenzweig C, Seguin B, Scholes RL, Whetton PH (contributing authors). Cambridge, UK: University of Cambridge Press. Available: http://www.ipcc-data.org/guidelines/ (March 2013).

Iverson LR, Schwartz MW, Prasad AM. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? Global Ecology and Biogeography 13:209–219.

Jackson ST, Betancourt JL, Booth RK, Gray ST. 2009. 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(Supplement 2):19685–19692.

Kampf SK, Burgess SJ. 2007. A framework for classifying and comparing distributed hillslope and catchment hydrologic models. Water Resources Research 43:W05423.

Keane RE, Cary GJ, Davies ID, Flannigan M, Gardner RH, Lavorel S, Lenihan JM, Li C, Rupp TS. 2004. A classifications of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecological Modelling 179:3–27.

Keane RE, Cary GJ, Parsons R. 2003. Using simulation to map fire regimes: an evaluation of approaches, strategies, and limitations. International Journal of Wildland Fire 12:309–322.

Keane RE, Loehman RA, Holsinger LM. 2011. The FireBGCv2 landscape fire and succession model: a research simulation platform for exploring fire and vegetation dynamics. Fort Collins, Colorado: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. General Technical Report RMRS-GTR-255 (see *Supplemental Material*, Reference S2, http://dx.doi.org/10.3996/062012-JFWM-055.S2); also available: http://www.firelab.org/research-projects/fire-ecology/139-firebgc (March 2013).

Kell LT, Pilling GM, O'Brien CM. 2005. Implications of climate change for the management of North Sea cod (*Gadus morhua*). ICES Journal of Marine Science 62: 1483–1491.

Knutti R, Furrer R, Tebaldi C, Cermak, J, Meehl GA. 2010. Challenges in combining projections from multiple climate models. Journal of Climate 23:2739–2758.

Knutti R, Sedlacek J. 2012. Robustness and uncertainties in the new CMIP5 climate model projections. Nature Climate Change 3:369–373.

Krawchuck MA, Cumming, SG. 2010. Effects of biotic feedback and harvest management on boreal forest fire activity under climate change. Ecological Applications 21:122–136.

Larocque GR, Archambault L, Delisle C. 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecological Modelling 222:2570–2583.

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.

Lawrence DM, Oleson KW, Flanner MG, Thornton PE, Swenson SC, Lawrence PJ, Zeng X, Yang Z-L, Levis S, Sakaguchi K, Bonan GB, Slater AG. 2011. Parameterization improvements and functional and structural advances in version 4 of the Community Land Model. Journal of Advances in Modeling Earth Systems 3: M03001.

Lawson DM, Regan HM, Zedler PH, Franklin A. 2010. Cumulative effects of land-use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. Global Change Biology 16:2518–2529.

Lenihan JM, Bachelet D, Neilson RP, Drapek R. 2008. Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. Climate Change 87:S215–S230.

Liang X, Lettenmaier DP, Wood EF, Burges SJ. 1994. A simple hydrologically based model of land surface water and energy fluxes for GSMs. Journal of Geophysical Research 99:14415–14428.

Littell JS, Gwozdz RB. 2011. Climatic water balance and regional fire years in the Pacific Northwest, USA: linking regional climate and fire at landscape scales. Pages 117–139 in McKenzie D, Miller C, Falk DA, editors. The landscape ecology of fire. Dordrecht, The Netherlands: Springer.

Littell JS, McKenzie D, Kerns BK, Cushman SA, Shaw CB. 2011. Managing uncertainty in climate-driven ecological models to inform adaptation to climate change. Ecosphere 2:102.

Littell JS, McKenzie D, Peterson DL, Westerling AL. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecological Applications 19: 1003–1021.

Martínez-Meyer E, Peterson AT, 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.

Maslin M, Austin P. 2012. Uncertainty: climate models at their limit? Nature 486:183–184.

Maurer EP. 2007. Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. Climatic Change 82:309–325.

Maurer EP, Brekke L, Pruitt T, Duffy PB. 2007. Fine-resolution climate change projections enhance regional climate change impact studies. Eos Transactions American Geophysical Union 88:504.

Maurer EP, Wood AW, Adam JC, Lettenmaier DP, Nijssen B. 2002. A long-term hydrologically-based data set of land surface fluxes and states for the conterminous United States. Journal of Climate 15:3237–3251.

McKelvey KS, Copeland JP, Schwartz MK, Littell JS, Aubry KB, Squires JR, Parks SA, Elsner MM, Mauger GS. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. Ecological Applications 21:2882–2897.

McKenzie D, Littell JS. 2011. Climate change and wilderness fire regimes. International Journal of Wilderness 17:22–27.

McKenzie D, Miller C, Falk DA. 2011. Toward a theory of landscape fire. Pages 3–26 in McKenzie D, Miller C, Falk DA, editors. The landscape ecology of fire. Dordrecht, The Netherlands: Springer.

Mclaughlin BC, Zavaleta ES. 2012. Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*). Global Change Biology 18:2301–2312.

McRae BH, Schumaker NH, McKane RB, Busing RT, Solomon AM, Burdick CA. 2008. A multi-model framework for simulating wildlife population response to land-use and climate change. Ecological Modelling 219:77–91.

Mearns LO, Gutowski W, Jones R, Leung S, McGinnis S, Nunes A, Qian Y. 2009. A regional climate change assessment program for North America. Eos Transactions American Geophysical Union 90:311.

Medvigy D, Wofsy SC, Munger JW, Hollinger DY, Moorcroft PR. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: ecosystem demography model version 2. Journal of Geophysical Research: Biogeosciences 114(G1).

Meehl GA, Covey C, Delworth T, Latif M, McAvaney B, Mitchell JFB, Stouffer RJ, Taylor KE. 2007. The WCRP CMIP3 multimodel dataset: a new era in climate change research. Bulletin of the American Meteorological Society 88:1383–1394.

Meehl GA, Goddard L, Murphy J, Stouffer RJ, Boer G, Danabasoglu G, Dixon K, Giorgetta MA, Greene AM, Hawkins E, Hegerl G, Karoly D, Keenlyside N, Kimoto M, Kirtman B, Navarra A, Pulwarty R, Smith D, Stammer D, Stockdale T. 2009. Decadal prediction, can it be skillful? Bulletin of the American Meteorological Society 90: 1467–1485.

Moorcroft PR, Hurtt GC, Pacala SW. 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). Ecological Monographs 71 557–586.

Morin X, Thuiller W. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90: 1301–1313.

Mote P, Brekke L, Duffy PB, Maurer E. 2011. Guidelines for constructing climate scenarios. Eos Transactions American Geophysical Union 92:257.

Noss RF, Franklin JF, Baker WL, Schoennagel T, Moyle PB. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment 4:481–487.

Pabst RJ, Goslin MN, Garman SL, Spies TA. 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. Forest Ecology and Management 256:958–972.

Parry ML, Canziani OF, Palutikof J, van der Linden PJ, Hanson CE, editors. 2007. Climate Change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on climate change. Cambridge, UK: Cambridge University Press. Available: http://www.ipcc.ch/publications_and_data/ar4/wg2/en/contents.html (March 2013).

Parton WJ, Morgan JA, Wang G, Del Grosso S. 2007. Projected ecosystem impact of the prairie heating and CO_2 Enrichment experiment. New Phytologist 174:823–834.

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.

Peeters F, Straile D, Lorke A, Livingstone DM. 2007. Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. Global Change Biology 13:1898–1909.

Peterson DL, Millar CI, Joyce LA, Furniss MJ, Halofsky JE, Neilson RP, Morelli T-L. 2011. Responding to climate change in national forests: a guidebook for developing adaptation options. Portland, Oregon: Pacific Northwest Research Station. USDA Forest Service General Technical Report PNW-GTR-855 (see *Supplemental Material*, Reference S3, http://dx.doi.org/10.3996/062012-JFWM-055.S3); also available: http://www.treesearch.fs.fed.us/pubs/39884 (March 2013).

Peterson GD. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. Ecosystems 5:329–338.

Peterson GD, Cumming GS, Carpenter SR. 2003. Scenario planning: a tool for conservation in an uncertain world. Conservation Biology 17:358–366.

Piao S, Friedlingstein P, Ciais P, de Noblet-Decoudré N, Labat D, Zaehle S. 2007. Changes in climate and land use have a larger direct impact than rising CO_2 on global river runoff trends. Proceedings of the National

Academy of Sciences of the United States of America 104:15242–15247.

Pierce DW, Barnett TP, Santer BD, Gleckler PJ. 2009. Selecting global climate models for regional climate change studies. Proceedings of the National Academy of Sciences of the United States of America 106:8441–8446.

Prasad AM, Iverson LR, Liaw A. 2006. Newer classification and regression tree techniques: bagging and random forests for ecological prediction. Ecosystems 9:181–199.

Quillet A, Peng C, Garneau M. 2010. Toward dynamic global vegetation models for simulating vegetation-climate interactions and feedbacks: recent developments, limitations, and future challenges. Environmental Reviews 18:333–353.

Ramirez J, Jarvis A. 2008. High Resolution Statistically Downscaled Future Climate Surfaces. International Center for Tropical Agriculture (CIAT); CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS). Cali, Colombia. Available: http://www.ccafs-climate.org (March 2013).

Ray JC. 2000. Mesocarnivores of northeastern North America: status and conservation issues. Working Paper No. 15. Wildlife Conservation Society, New York.

Rehfeldt GE, Crookston NL, Sáenz-Romero C, Campbell EM. 2012. North American vegetation model for land-use planning in a changing climate: a solution to large classification problems. Ecological Applications 22:119–141.

Roe GH, Baker MB. 2007. Why is climate sensitivity so unpredictable? Science 318:629–632.

Rogers BM, Neilson RP, Drapek R, Lenihan JM, Wells JR, Bachelet D, Law BE. 2011. Impacts of climate change on fire regimes and carbon stocks of the U.S. Pacific Northwest. Journal of Geophysical Research 116: G03037.

Rolls RJ, Leigh C, Sheldon F. 2012. Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. Freshwater Science 31:1163–1186.

Salathe EP, Mote PW, Wiley MW. 2007. Review of scenario selection and downscaling methods for the assessment of climate change impacts on hydrology in the United States Pacific Northwest. International Journal of Climatology 27:1611–1621.

Sakaguchi K, Zeng Z, Brunke MA. 2012. The hindcast skill of the CMIP ensembles for the surface air temperature trend. Journal of Geophysical Research 117:113.

Scheuerell MD, Hilborn R, Ruckelshaus MH, Bartz KK, Lagueux KM, Haas AD, Rawson K. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish-habitat relationships in conservation planning. Canadian Journal of Fisheries and Aquatic Sciences 63:1596–1607.

Schloss CA, Nuñez TA, Lawler JJ. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences of the United States of America 109:8606–8611.

Schumaker NH, Ernst T, White D, Baker J, Haggerty P. 2004. Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. Ecological Applications 14:381–400.

Seidl R, Fernandes PM, Fonseca TF, Gillet F, Jönsson AM, Merganičová K, Netherer S, Arpaci A, Bontemps JD, Bugmann H. 2011. Modelling natural disturbances in forest ecosystems: a review. Ecological Modelling 222: 903–924.

Smith B, Prentice IC, Sykes MT. 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Global Ecology and Biogeography 10:621–637.

Smucker KM, Hutto RL, Steele BM. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15:1535–1549.

Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, editors. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press. Available: http://www.ipcc.ch/publications_and_data/ar4/wg1/en/contents.html (March 2013).

Stocks BJ, Mason JA, Todd JB, Bosch EM, Wotton BM, Amiro BD, Flannigan MD, Hirsch KG, Logan KA, Martell DL, Skinner WR. 2002. Large forest fires in Canada, 1959–1997. Journal of Geophysical Research 107:8149.

Swetnam TW, Betancourt JL. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climate 11:3128–3147.

Tague C, Band L. 2004. RHESSys: regional hydro-ecologic simulation system: an object-oriented approach to spatially distributed modeling of carbon, water and nutrient cycling. Earth Interactions 8:1–42.

Taylor KE, Stouffer RJ, Meehl GA. 2012. An overview of CMIP5 and the experiment design. Bulletin of the American Meteorological Society 93:485–498.

Tebaldi C, Knutti R. 2007. The use of the multi-model ensemble in probabilistic climate projections. Philosophical Transactions of the Royal Society. Series A: Mathematical and Physical Sciences 365:2053–2075.

Thuiller W. 2004. Patterns and uncertainties of species' range shifts under climate change. Global Change Biology 10:2020–2027.

Turner MG, Romme WH. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9:59–77.

VanShaar JR, Haddeland I, Lettenmaier DP. 2002. Effects of land-cover changes on the hydrological response of interior Columbia River basin forested catchments. Hydrological Processes 16:2499–2520.

Vicuna S, Maurer EP, Joyce B, Dracup JA, Purkey D. 2007. The sensitivity of California water resources to climate change scenarios. Journal of the American Water Resources Association 43:482–498.

Viney NR, Bates BC, Charles SP, Webster IT, Bormans M. 2007. Modelling adaptive management strategies for coping with the impacts of climate variability and change on riverine algal blooms. Global Change Biology 13:2453–2465.

Weigel AP, Knutti R, Liniger MA, Appenzeller C. 2010. Risks of model weighting in multimodel climate projections. Journal of Climate 23:4175–4191.

West JM, Julius SH, Kareiva P, Enquist C, Lawler JJ, Peterson AE, Johnson E, Shaw MR. 2009. U.S. natural resources and climate change: concepts and approaches for management adaptation. Environmental Management 44:1001–1021.

Westerling AL, Bryant BP. 2007. Climate change and wildfire in California. Climatic Change 87:231–249.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. 2006. Increases in Western US forest wildfire associated with warming and advances in the timing of spring. Science 313:940–943.

Wigmosta MS, Vail LW, Lettenmaier DP. 1994. A distributed hydrology–vegetation model for complex terrain. Water Resources Research 30:1665–1679.

Williams JW, Jackson ST. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5:475–482.

Williams JW, Kharouba HM, Veloz S, Vellend M, McLachlan J, Liu Z, Otto-Bliesner B, He F. 2013. The ice age ecologist: testing methods for reserve prioritization during the last global warming. Global Ecology and Biogeography 22:29–201.

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:e325–e325.

Yates D, Sieber J, Purkey DR, Huber-Lee A. 2005. WEAP21: a demand-, priority-, and preference-driven water planning model: part 1, model characteristics. Water International 30:487–500.

Zarnetske PL, Skelly DK, Urban MC. 2012. Biotic multipliers of climate change. Science 336:1516–1518.