# IV. Peering into the Future: Climate and Ecological Models

Assessing the exposure of species to climate change requires the ability to peer into the future and identify likely or potential changes in ecologically relevant variables. These variables can be both direct climatic factors, such as changes in temperature or precipitation, or indirect factors, such as shifts in ecosystem processes or interactions with other species. Models provide an important means for forecasting possible future conditions. A model constitutes a representation of a system, which enables researchers to investigate and understand the properties of that system. Depending on their design, models can also be used to simulate future conditions and outcomes. Although models can be powerful, they also have limitations. The statistician George Box famously has been quoted as saying "all models are wrong, but some are useful" (Box and Draper 1987). Considerable progress has been made over the past few decades, however, in developing robust and useful models for understanding both the earth's climate systems, as well as the ecological responses to climate.

This chapter provides an overview of the types of climate and ecological response models that are relevant to vulnerability assessments of species, habitats, or ecosystems. The purpose of reviewing these models is not to suggest that all vulnerability assessments will be involved in running these models: rather, it is to ensure that assessors are knowledgeable about the range of models available, and can be well-informed consumers, understanding the basis for and assumptions underlying widely used models. In particular, most vulnerability assessments will not involve running sophisticated and complex global climate change models, but will instead rely on existing scenarios and make use of available downscaled climate projections. Assessments more often will rely on application of ecological response models, although even those models may be supplanted or bolstered by existing studies in the scientific literature or by means other than modeling (e.g., expert elicitation).

## Climate Models

Increasing emissions of $CO_2$, methane, and other heat-trapping greenhouse gases are perturbing average climate conditions at local to global scales in ways that cannot be predicted by the past. Instead, projections of future climate conditions rely on climate model simulations driven by assumptions about how population, energy use, and technology are likely to develop in the future. These assumptions are collectively known as *emission scenarios*, as they serve as the basis to estimate the emissions of greenhouse gases, particulates, and other pollutants that would result.

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Emission scenarios are then used as inputs to global climate models in order to simulate the changes in temperature, precipitation, and other aspects of climate likely to result from that set of assumptions. Global climate models represent climate at a relatively coarse resolution and they do not resolve differences in climate variables at scales finer than several hundred kilometers. The "basic" global climate models are the General Circulation Models (GCM), which are mathematical models of a planetary atmosphere or ocean based on given equations for physics, fluid motion, and chemistry. At the most comprehensive end of the spectrum are the coupled Atmosphere–Ocean General Circulation Models (AOGCM), which address additional factors such as models for sea ice or evapotranspiration over land.

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Output from global climate model simulations can be used to calculate regional trends, but these are difficult to incorporate directly into planning efforts. For this reason, a range of downscaling techniques have been developed. Although downscaled climate projections often provide the spatial and temporal resolution needed to assess the impacts of climate change on a given region or system, it is important to understand the limitations of these data as well. Downscaled projections are uncertain for the same reasons as global projections: the range in plausible future scenarios; the sensitivity of the climate system to those emissions; our imperfect understanding of and ability to model the climate system; the natural variability of the climate system; and the degree to which the simulations are able to capture the relationship between local climate and large-scale drivers.

Due to the uncertainty inherent in future projections, multiple future scenarios should be considered in impact assessments. In an area where precipitation trends are highly uncertain, for example, a state might choose to consider two scenarios: one warmer and wetter, and one warmer and drier. Adaptation strategies that are robust to multiple likely climate change scenarios would be considered "no regrets" strategies. In some instances, expert opinion can be useful for assessing the likelihood of how future local climates will reflect regional projections or how habitats will change. Expert opinion should be accompanied by an estimate of certainty and description of the assumptions, evidence, or reasoning underlying the opinion.

## Historical and Future Scenarios

### Control Scenarios

Climate models are not rigidly controlled by boundary conditions, as are response models. Rather, they generate their own internal natural variability. Before they can be run in transient mode (i.e., generating information for real calendar years),

climate model simulations begin with a long, time-independent control run. External forcing mechanisms (e.g., the strength of the sun and the concentrations of key atmospheric gases and aerosols) are set to preindustrial conditions and the model is run for several hundred years in order to "spin up" to the equilibrium condition in which our planet exists.

This is an essential step as climate models are, at their most basic level, simply numerical approximations of the fundamental laws of physics that govern nature at the scale of the planet, including conservation of momentum, conservation of mass and energy, and the four laws of thermodynamics. Control runs are not intended to be used by anyone outside the modeling community; their purpose is to establish a baseline set of model conditions that can be used to initiate a transient simulation beginning in preindustrial times and moving forward in to the future.

### Historical Scenarios

Once a preindustrial control run has been completed for any given climate model, a transient (time-dependent) simulation can be run, beginning in the year that was used to set conditions for the control run. This initial year varies from about 1850 to 1890, depending on the global modeling group. Historical scenarios run from the beginning year, in the 1800s, through 1999. Each month, external forcing mechanisms observed or measured for that month in the past are input to the models. These observed drivers can include changes in solar radiation, volcanic eruptions, human emissions of greenhouse gases and other radiatively active species, and secondary changes in ozone and water vapor.

Collectively, these historical total (human and natural) forcing scenarios are known as the "20th Century Climate in Coupled Models" or 20C3M scenarios in the IPCC AR4. These historical 20C3M scenarios are essential as they provide a baseline of observed climate against which future climate change can be quantified. Future climate projections should never be compared directly to historical observations in order to calculate the amount of change that may occur, as even the best models contain biases relative to observations. Rather, future projections must be compared to historical simulations, as biases are assumed to remain relatively constant over time. This change, or delta, provides the most reliable information on future change.

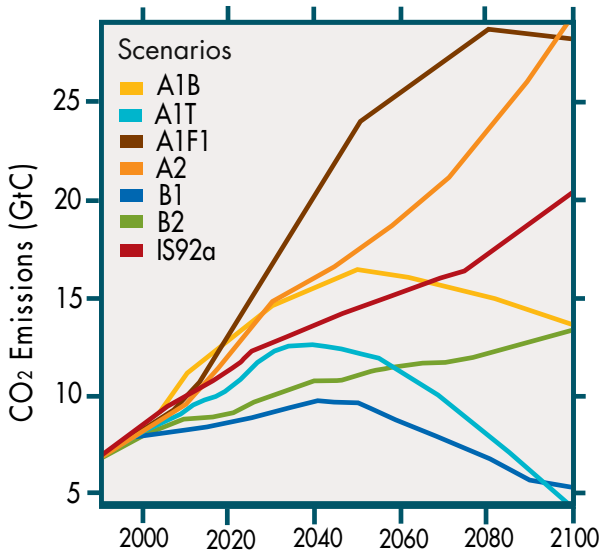


Figure 4.1. Projected future carbon emissions for the SRES emission scenarios. Emissions for the highest scenario (A1FI) correspond to the red dotted line at the top, while emissions for the lowest (B1) scenario are indicated by the solid green line (Nakicenovic et al. 2000).

## Emissions Scenarios

To estimate potential climate changes through 2100, we need to ask:

- How will human societies and economies evolve over the coming decades?

- What technological advances are expected, and how will they affect emissions?

- Which energy sources will be used in the future to generate electricity, power transportation, and serve industry?

The answers to these questions will affect future emissions of greenhouse gases from human activities. And these emissions will in turn determine future climate change at both the global and the regional levels.

To address these questions, in 2000 the IPCC developed a set of future emissions scenarios known as SRES (Special Report on Emissions Scenarios) (Nakicenovic et al. 2000). These scenarios use a wide range of projections for future population, demographics, technology, and energy use to estimate the greenhouse gas emissions that would result from a variety of possible futures. In doing so, they cover a wide range of plausible futures that illustrate differences in the extent and severity of the global warming that result from alternative emissions choices (Figure 4.1).

For example, the SRES higher-emissions or fossil-intensive scenario (A1FI) represents a world with fossil fuel–intensive economic growth and a global population that peaks mid-century and then declines. New and more efficient technologies are introduced toward the end of the century. In this scenario, atmospheric $CO_2$ concentrations (the amount of $CO_2$ in the atmosphere as a result of emissions) reach 940 ppm by 2100—more than triple preindustrial levels.

The lower-emissions scenario (B1) also represents a world with high economic growth and a global population that peaks mid-century and then declines. However, this scenario includes a shift to less fossil fuel–intensive industries and the introduction of clean and resource-efficient technologies. Emissions of greenhouse gases peak around mid-century and then decline. Atmospheric $CO_2$ concentrations reach 550 ppm by 2100—about double preindustrial levels.

## Concentration Pathways

New Representative Concentration Pathways (RCP) (Moss et al. 2010) are under development for the IPCC Fifth Assessment Report (AR5). In contrast to the SRES scenarios used in the AR4, the RCPs are expressed in terms of carbon dioxide equivalent ($CO_2$-eq) concentrations in the atmosphere, rather than direct emissions.

Although climate model simulations are not yet available for the RCPs, it is still possible to place SRES-based projections into the context of these new scenarios by converting the SRES emission scenarios to $CO_2$-eq concentrations. When we do that using the simple energy-balance climate model MAGICC (Model for the Assessment of Greenhouse-gas Induced Climate Change), we see that the highest RCP 8.5 corresponds closely to the higher SRES A1FI emissions scenario, with end-of-century $CO_2$-eq concentrations of 1465 ppm for RCP 8.5 as compared to 1360 ppm for A1FI (Figure 4.2) (Wigley 2008). In contrast, the lowest RCP 2.6 projects

a future where emissions are reduced significantly below even the lowest of the SRES scenarios, with $CO_2$-eq concentrations rising to nearly 500 ppm then falling to 450 ppm by the end of the century. The mid-low RCP 4.5 corresponds most closely to SRES B1, with $CO_2$-eq concentrations of nearly 600 ppm by the end of the century as compared to 640 ppm for B1.

Figure 4.2 is an important comparison as it enables the climate model projections currently available (and indeed, all that will be available through 2012) to be placed in the context of the next generation of climate scenarios. It also reveals that the substantial difference between the SRES A1FI and B1 scenarios, although conservative in comparison to the RCPs in its estimate of the lower end of the range of future emissions, is still sufficient to illustrate the potential range of changes that could be expected, and how these depend on energy and related emission choices made over coming decades.

## Uncertainties in Future Scenarios

It is important to note that, as broadly separated as they are, neither the SRES nor the RCP scenarios cover the entire range of possible futures. While the recent economic decline slowed $CO_2$ emissions growth rates in comparison to previous years, actual emissions remain near the top of the range of IPCC scenarios for the period 2000 to 2010 (Manning et al. 2010).

On the other hand, significant reductions in emissions, on the order of 80 percent below 1990 levels or more, could stabilize $CO_2$ levels below the lowest SRES emission

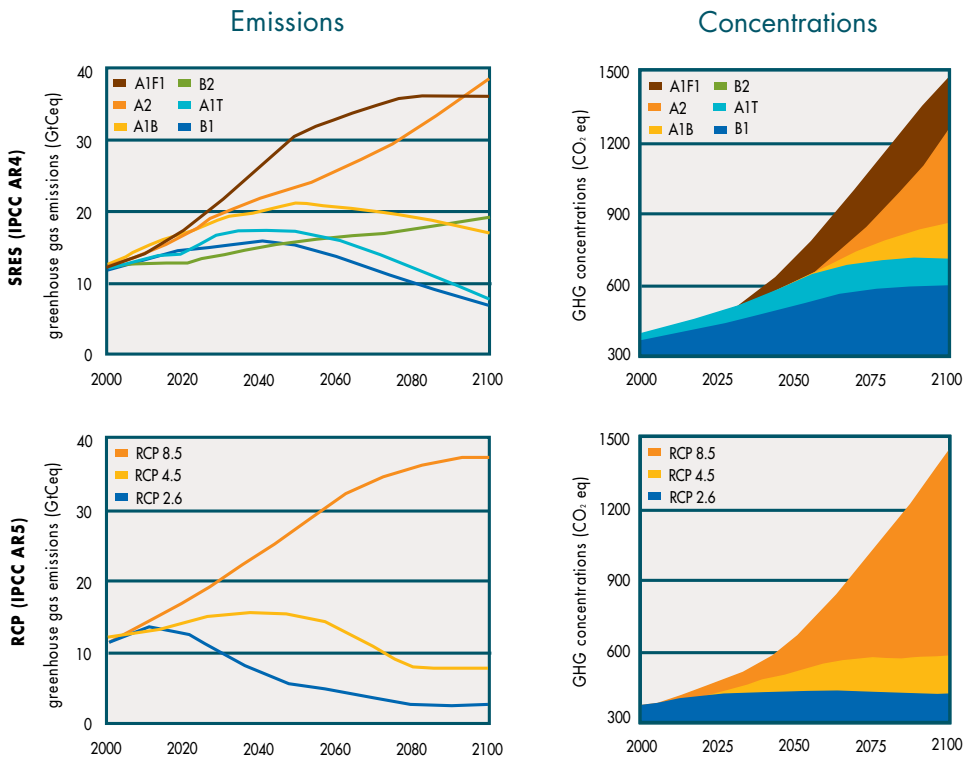


Figure 4.2. Projected future $CO_2$-equivalent emissions and concentrations for the SRES emission scenarios (IPCC AR4) and Representative Concentration Pathways (IPCC AR5).

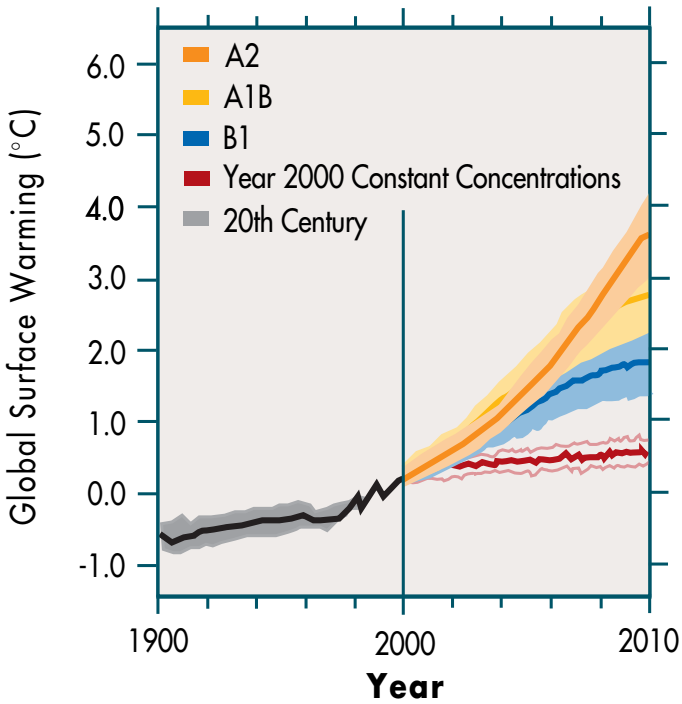


Figure 4.3. Projected future global temperature change for the SRES emission scenarios (degrees Celsius). The range for each individual emission scenario indicates model uncertainty in simulating the response of the earth system to human emissions of greenhouse gases (IPCC 2007b).

scenario (e.g., Meinshausen et al. 2006). Such policy options were not considered in the SRES scenarios, although the new RCPs (Moss et al. 2008, 2010) currently under development for the IPCC Fifth Assessment Report at least partially address this issue.

## Global Climate Models

### Description

Emissions or concentration scenarios are used as input to global climate models, which vary in complexity. The most complex are the AOGCMs. These are large, three-dimensional coupled models that incorporate the latest understanding of the physical processes at work in the atmosphere, oceans, and earth's surface. As output, AOGCMs produce geographic grid-based projections of precipitation, temperature, pressure, cloud cover, humidity, and a host of other climate variables at daily, monthly, and annual scales.

Because of the complexity of these models, they are generally designed and run by large research teams at supercomputing centers. Models are constantly being enhanced as scientific understanding of climate improves and as computational power increases. Over time, the number of global climate models has grown. By 2008, 16 international climate modeling teams had submitted historical and future simulations from 25 different climate models to the IPCC's AR4. All future simulations by these models agree that both global and regional temperatures will increase over the coming century in response to increasing emissions of greenhouse gases from human activities (Figure 4.3).

### Model Selection

Some models are more successful than others at reproducing observed climate and trends over the past century in particular geographic regions. Inter-model comparisons (e.g., Kunkel et al. 2006; Wang et al. 2007; Stoner et al. 2009) generally find that climate models tend to fall into three broad categories: "good" models that are able to simulate important climate features, from Arctic weather systems to natural variability such as El Niño, across the globe; "fair" models that perform well in some regions and at some tests, but poorly in others; and "poor" models, usually those in relatively early stages

of development, that consistently fail to reproduce fundamental aspects of the earth's climate system.

For the purposes of global climate model selection for impact analyses, however, the most relevant point is that multi-model comparisons have shown that, for a given emissions scenario, the average of multiple models generally provides a more robust picture of future conditions than any one model (Tebaldi and Knutti 2007). Moreover, evaluating which set of models may be "best" at simulating future trends over any given region and for a certain variable is a long and involved process, generally requiring a fundamental understanding of climate dynamics that have contributed to climate variability and long-term trends over the region of interest. (Although simple biases or differences between models and observations have been used in the past to judge which models are "better" than others, this practice is highly discouraged as the information derived from such a calculation bears little relevance to actual model performance in simulating climate change and may mislead more than it may guide.) So in evaluating the potential impacts of climate change on any given region, it is always best to use the average of multiple global climate models rather than to rely on one or two. As it may not be possible to use all global climate model simulations, some general criteria for model selection are the following:

- Consider only well-established models, whose strengths and weaknesses are already extensively described and evaluated in the peer-reviewed scientific literature. The models should have participated in the Coupled Model Intercomparison Project (CMIP; http://cmip-pcmdi.llnl.gov/) or otherwise been evaluated and shown to adequately reproduce key features of the atmosphere and ocean system. Key features include seasonal circulation patterns, atmosphere–ocean heat fluxes, El Niño, and other teleconnection patterns affecting climate in the region (Covey et al. 2003; AchutaRao and Sperber 2002; Chapman and Walsh 2007; DeGaetano et al. 2008; Vrac et al. 2006).

- The models chosen should encompass the greater part of the range of uncertainty in climate sensitivity simulated by global climate models. Because many of the processes at work in the earth–atmosphere system are not yet fully understood, these are represented somewhat differently in different global climate models. A range in projected temperature change and other climate variables arise from the different climate sensitivity of the models.

- From a purely practical perspective, the projections required for the impact analysis must be available from that model, preferably for multiple future scenarios in order to encompass the uncertainty in predicting future drivers of change.

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## Box 4.1. How Much Sea-Level Rise Should We Plan For?

Asking how much sea-level rise to assume in coastal vulnerability assessments is a common question, but not necessarily straightforward to answer. As with modeling the climate system itself, projecting how much global sea levels will rise due to global warming is complex, and there are many sea-level rise scenarios in the literature. In general, global sea-level rise figures refer to changes in eustatic sea level, referring to changes in the volume of seawater. For planning purposes, it is important to recognize that a number of other factors affect the amount of relative sea-level change experienced in a given area. Local land subsidence, for example, will mean that the rate of relative sea-level rise in that area will be higher than the eustatic rate. Nevertheless, projections for eustatic sea level are an important baseline for assessing coastal vulnerability.

Modeling eustatic sea level requires integrating factors such as thermal expansion of the oceans as well as rates of change of land-based ice, including glaciers and continental ice sheets, all of which are subject to uncertainties. Some of the most widely used scenarios are from the IPCC, whose most recent estimates range from an additional 7 to 23 inch rise in global average sea level over 1990 levels by the 2090s (IPCC 2007b). There is compelling new evidence, however, that because these figures ignore recent dynamic changes in Greenland and Antarctica ice flow, they underestimate the rate of sea-level rise that we are likely to experience during this century (Overpeck and Weiss 2009; Pfeffer et al. 2008). Taking at least some of this accelerated melting into account, Vermeer and Rahmstorf (2009) suggest that a feasible range might be 30 to 75 inches for the period 1990-2100. Complicating matters, the magnitude of sea-level rise will not be globally uniform because of ocean circulation patterns and the earth's rotation, gravitational differences, local and regional geological differences, and other factors (Bamber et al. 2009; Mitrovika et al. 2009; Church et al. 2004; Yin et al. 2009).

Ultimately, choosing which scenarios upon which to base vulnerability assessments and associated climate change adaptation strategies will depend on how much risk we are willing to accept. When relatively little is at stake in the way of infrastructure investment or public inconvenience, we could choose to design for a conservative or low-end sea-level rise scenario. Where more is at stake, such as the decimation of habitats critical to a region's ecological and economic well-being, we might design for a mid-range or aggressive sea-level rise scenario. The bottom line, however, is that we may never know with certainty how much or how fast sea level will rise. Accordingly, using a range of scenarios in your assessment might be the optimal approach.

- Finally, note that within any climate model, uncertainties will vary for different simulated phenomena. For example, large-scale surface temperature is generally trusted more than precipitation, which requires many physical processes to be simulated correctly at the same time and place.

## Downscaling of Global Model Simulations

The geographic grid cells that form the basis of AOGCMs typically range in size from about 160 to 800 kilometers per side. In general, this type of resolution

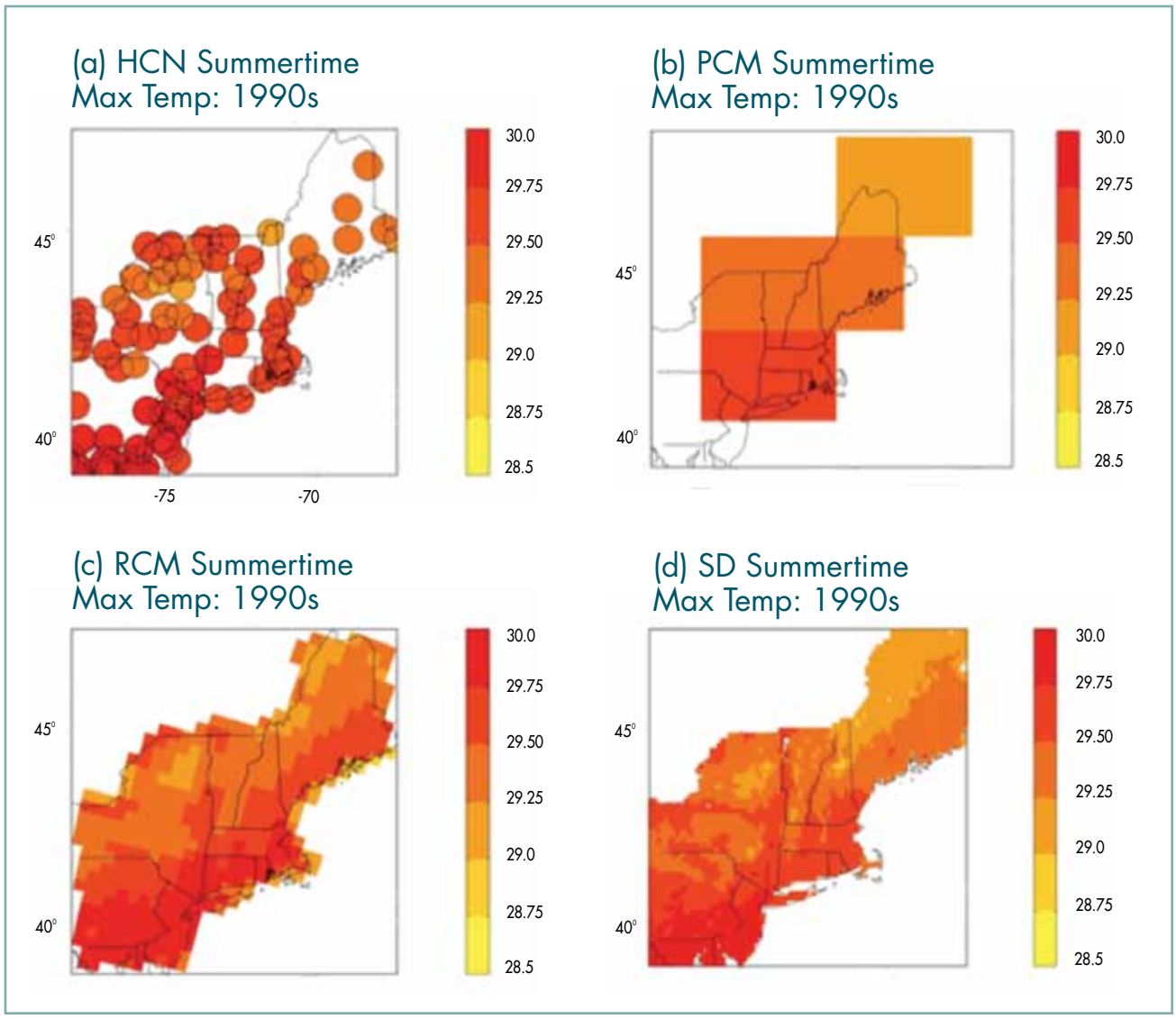


Figure 4.4. Average summer maximum temperature in the U.S. Northeast for the 1990s, based on (a) observations from weather stations in the Historical Climatology Network, (b) the global climate model PCM, (c) regional climate model simulations, and (d) statistically downscaled simulations. From Hayhoe et al. 2008.

is too coarse to capture the fine-scale changes experienced at the regional scale. For this reason, a number of downscaling techniques have been developed to transform global climate model output into higher-resolution projections capable of resolving the impacts of climate change on local conditions.

### Dynamical Downscaling

Dynamical downscaling, or regional climate modeling, uses a high-resolution climate model centered over a relatively small region and driven by global climate model output fields at its boundaries. Model grid cells range from 10 to 50

kilometers, and contain substantially different physics than the global models in order to resolve the physical processes that occur at spatial scales below those of the global models. Regional climate models are able to simulate the dynamic changes in climate likely to occur as global climate changes; however, regional climate model simulations are expensive to run and few global climate models save the high-resolution temporal fields (at 3 or 6 hours) required to drive the regional models. Hence, regional model simulations tend to be limited to specific timeslices from future decades, rather than a continuous time period, and tend to be driven by several global models rather than the full suite of IPCC global climate models. The most comprehensive set of regional model simulations has been generated by the North American Regional Climate Change Assessment Program (NARCCAP), which uses four regional model–global model pairs to simulate conditions for 2041 to 2070 compared to 1971 to 2000.

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### Statistical Downscaling

Statistical downscaling relies on historical instrumental data for calibration at the local scale. A statistical relationship is first established between AOGCM output for a past "training period," and observed climate variables of interest (here, daily maximum and minimum temperature and precipitation). This relationship is averaged over at least two decades to remove year-to-year fluctuations. The historical relationship between AOGCM output and monthly or daily climate variables at the regional scale is then tested using a second historical "evaluation period" to ensure the relationship is valid. If so, then the relationship is finally used to downscale future AOGCM simulations to that same scale.

Unlike regional climate modeling, statistical downscaling assumes that the relationships between large- and small-scale processes remain fixed over time. This assumption may not always be justified, particularly for precipitation. However, analysis of 37 stations in the state of Illinois suggests that this relationship only breaks down for the most extreme precipitation events above the 99th percentile of the distribution (Vrac et al. 2006). Analyses for the Northeast (Hayhoe et al. 2008) further indicate that, in areas of variable topography such as mountains and coastlines, statistical methods trained to match historical spatial patterns may perform better than regional climate models that are limited by their convection schemes (see Figure 4.4). In addition, statistical downscaling has a substantial time and cost advantage; hundreds of years of model simulations can be downscaled using the same computing resources required to run only a few

years of regional-model downscaling. Three of the case studies in Chapter VII use statistical downscaling for climate change data. Case Studies 1, 3, and 6 rely on a tool called the ClimateWizard (www.climatewizard.org), which was developed by The Nature Conservancy, University of Washington, and University of Southern Mississippi to enable technical and nontechnical users to access historical and projected climate change information for a given area based on downscaled data from a range of climate models, emissions scenarios, and time periods. In Case Study 7, researchers will be conducting their own statistical downscaling projections for at least six future climate projections.

## Ecological Response Models

Ecological response models are a critical part of the overall vulnerability assessment process. They provide a way to assess the sensitivity and potential adaptability or resilience of wildlife species, habitats, and ecosystems to climate change (Wormworth and Mallon 2007). They also are fundamental to understanding the kinds of climate variables that are needed to conduct vulnerability assessments. As such, information from response models enhances the iterative dialog between biologists/ecologists and climatologists such that downscaled climate change variables address the most appropriate scales (temporal and spatial) and scope (types of variables that relate to sensitivity and/or resilience) needed to conduct the vulnerability assessment. This dialog is critical in identifying the spatial extent of the downscaled climate information that will then be used to assess exposure of species, habitats, and ecosystems. Moreover, response models help identify indicators and potential thresholds or tipping points that can be used in vulnerability assessments (Bradley and Smith 2004; Groffman et al. 2006).

The decision on which model or combinations of models to use depends on the species, habitats, and ecosystems of concern, the types of questions being asked, and the particular end-users' needs. The local geographic and biophysical characteristics of habitats and ecosystems require the use of response models that are well suited to the specific environmental settings (Primack et al. 2009). Moreover, the type of questions and needs associated with the vulnerability assessment affect the scale and scope of the assessment. The objective of some vulnerability assessments is to target species or geographic areas where species, habitats, and/or ecosystems are potentially most vulnerable to declines in conditions due to climate change (Bradley and Smith 2004). These types of vulnerability assessments are usually conducted at large basin or regional scales, and the results are used to target species and geographic areas where further attention (data gathering, modeling, etc.) is needed. Other vulnerability assessments rely on more complex models involving specific species or habitats in specific geographies, as well as a range of species traits and processes (Martin 2007).

An important part of model selection and/or development process is to clearly identify the endpoints of interest. Endpoints are definable and measurable aspects of the environment upon which environmental assessments are made. Lack of clear endpoints often reduces the

relevance and utility of the assessment results (Boyd 2007). In some cases, species' vulnerabilities are assessed because they are the endpoint (e.g., a species listed through the ESA) or because they affect ecosystem functions (e.g., an invasive species as it affects fire disturbance regimes) (Hunter 2007).

## Types of Response Models

This section briefly describes different types of response models and how they are generally used. Different approaches are often used in combination (Martinez-Meyer 2005), but for clarity we provide basic descriptions of each.

### Conceptual Models

Conceptual models are qualitative descriptions and diagrams of key attributes and processes related to specific species, habitats, or ecosystems of concern (see Schlesinger et al. 1990 for an example related to desertification). They also illustrate or describe important linkages to stressors, such aspects of climate and land use, and how changes in stressors affect important attributes (e.g., soil texture) and functions (nutrient uptake, water flux, etc.). These linkages to stressors provide the basic information needed to assess vulnerability (e.g., sensitivity), and help inform the spatial extent of the stressor needed to analyze exposure. Nearly all types of other response models are built from well-conceived conceptual models as they help identify key variables in models needed to assess sensitivity and exposure. For a review of conceptual model development see Heemskerk et al. (2003). Various types of conceptual modeling tools and software can be found at http://www.fileheap.com/software/conceptual_data_model.html.

### General Characterization Models

Characterization models usually represent broad groups (e.g., amphibians, riparian species) or generalized traits to identify how groups of species might respond to climate and/or habitat change. These models can be fairly simple. For example, they can involve groupings of species based on their preference for certain habitats. Or, they can involve species grouped by physiological, functional, and/or other biological traits, and their potential sensitivity (response) to specific aspects of climate change (Lavorel et al. 1997). In most cases, spatial distribution of sensitivity is estimated by applying the classes of vulnerability (characterization part) to species distribution maps (Lavorel et al. 1997). Another characterization approach involves meta-analyses whereby existing studies are pooled together to estimate common responses of species (Parmesan and Yohe 2003; Allen et al. 2010). These can be especially effective at validating responses over large areas. The NatureServe Climate Change Vulnerability Index is an example of an easy-to-use characterization tool to assess vulnerability (http://www.natureserve.org/prodServices/climatechange/ClimateChange.jsp) (see Case Study 1).

### Expert Opinion Models

These models are constructed from the opinions of experts on a particular species, habitat, or ecosystem. They are often used when existing data preclude or are insufficient to develop a quantitative

model. A series of workshops and/or surveys are often used to gather data from experts that are then used in model development. In some cases results from expert input are combined with other data (e.g., from existing publications). Statistical approaches (e.g., Bayesian statistics) are often used to combine these data from different sources to produce estimates of potential responses and uncertainty (Berliner et al. 2000; Prato 2009). Expert opinion is often used in assembling conceptual models (see previous discussion). There are many software modules that can be downloaded to assist in development of expert opinion models. Some examples include the Bayesian Analysis Toolkit (http://www.mppmu.mpg.de/bat/), Treeage Pro software (http://www.treeage.com/products/index.html), and the Delphi Decision Aid site (http://armstrong.wharton.upenn.edu/delphi2/).

### Habitat and Occupancy Models

Habitat and occupancy models are perhaps the most common models used to address potential vulnerability of species to climate and land-use change. Some habitat models, such as those that have been developed by the U.S. Geological Survey GAP model habitat suitability over large geographic areas based on the development of habitat criteria (developed mostly from expert opinion and published literature). These requirements (rules) are expressed as ranges in specific biophysical attributes (e.g., climate, soils, vegetation or land cover, elevation, etc.) that a species will occupy (e.g., "suitable" habitat). The requirements (range of biophysical conditions) are then applied to wall-to-wall biophysical data, such as through Geographic Information System (GIS) coverages or grids, to determine the spatial distribution of suitable habitat for individual species. In a few cases, species ranges and suitable habitat have been defined largely by climate variables (e.g., Climate Envelope models) (Harrison et al. 2006; Pearson and Dawson 2003). In these cases, species sensitivities and vulnerability can be directly assessed with climate data. In cases where suitability is defined by vegetation or land cover attributes (including distribution), models of habitat shifts associated with climate change scenarios are needed to conduct the assessment (Johnson et al. 2005).

One example of this type of model is the Sea Level Affecting Marshes Model (SLAMM), in which a flexible and complex decision tree incorporating geometric and qualitative relationships is used to represent transfers among coastal habitat classes under various scenarios of sea-level rise (Clough et al. 2010). Case Study 5 uses SLAMM (Version 5.0) in an assessment of coastal habitat vulnerability in the Chesapeake Bay region. Vegetation- and habitat-associated response to climate change seem to be the most prevalent type of response model used to evaluate potential effects of climate change on species.

Niche-based models are also used to estimate species distributions and habitat suitability, but they generally involve more quantitative approaches with estimates of the probability of occurrence of a species. Approaches such as Genetic Algorithm for Rule-set Production (GARP) (Stockwell and Peters 1999) and Maximum Entropy modeling (Maxent) (Phillips et al. 2006) are examples of niche-based models. Niche and occupancy models produce probabilities of occurrence using locations records of species (e.g., from museum records,

systematic surveys, and other databases) and wall-to-wall biophysical data such as elevation, topography, temperature, precipitation, soils, and geology to name a few (Ballesteros-Barrera et al. 2007). As such, they define the "habitat niche" of the species. Other statistical models incorporate approaches like Regression Tree and Random Forests (O'Connor et al. 1996; Lunetta et al. 2004; Garzón et al. 2006). These also can be used to access habitat suitability for species, but have the advantage of being able to assess how the importance of biophysical attributes change among different geographies (O'Connor et al. 2006).

When climate change variables are important attributes of these models, direct responses to different climate change scenarios can be assessed statistically. When biophysical attributes such as vegetation and land cover are the most important variables, species responses to climate change are evaluated by applying models of vegetation and/or land cover responses to climate. Statistical functions generated from these models result from spatial variation and not the responses of species and habitats to climate change over time. That is, they use spatial variability to determine how species and habitats might respond to climate change. However, recently, phylogenetic and phylogeographic analyses have been used in combination with niche-based models to improve response models by adding a historical response component (Waltari et al. 2007). These analyses use molecular markers and tree-based statistical approaches to determine how species have responded (diversification, range contraction, etc.) to historical climate change.

Software used to develop niche and occupancy models can be downloaded for free from the Internet, including GARP (http://www.nhm.ku.edu/desktopgarp/), Maxent (http://www.cs.princeton.edu/~schapire/maxent/), Regression Trees and Random Forests (http://rattle.togaware.com/rattle-download.html), and Bioclim (http://software.informer.com/getfree-bioclim-download-software/). Additionally, many of the species models developed by the GAP program can also be downloaded, including biophysical data (http://www.nbii.gov/portal/server.pt/community/maps_and_data/1850/species_modeling/7000).

### Vegetation/Habitat Response Models

Many of the approaches and models described for animal species above are also used to estimate potential response of plants to climate change (Lawler et al. 2006). However, because of greater depth of historical records for plants (e.g., pollen records), it is often possible to refine plant and vegetation response models using historical records (Cole 2010). Moreover, plant and vegetation distribution records are considerably more abundant than animal records and, therefore, are easier to model using statistical approaches (Van Mantgem et al. 2009). Vegetation and plant community models are critically important to assess animal species changes, especially when animal distributions and habitat suitability are defined by vegetation and plant community variables. Robinson et al. (2008) provide an extensive review of vegetation climate models, broadly grouped into statistical species distribution models, GAP models, landscape models, biogeochemical models, and dynamic global vegetation models.

## Physiologically Based Models

Physiologically based response models incorporate sensitive aspects of individual species physiologies that influence foraging, nesting/reproduction, thermoregulation, and migration (Root 1988a and 1988b; Martin 2001; Reist et al. 2006; Bernardo et al. 2007; Hunter 2007). Broad-scale changes in species distributions have been tied closely to physiological constraints (Root et al. 2003). The aim is to relate the physiological traits and processes to climate change variables. These models can be used as part of general characterization models or as part of habitat models (Root et al. 2003; see earlier discussions). More complex models quantify interactions between key physiological variables and other variables, such as behavior, growth, and survival, and how important climate variables such as temperature affect interactions (Biro et al. 2007). However, complex models of these types are difficult to build over large areas because of the amount and type of data needed (e.g., data on movement patterns, behavior, growth, survival, etc.). Therefore, these models are most commonly built for specific species in specific geographies. We are unaware of any off-the-shelf software or tools that permit development of physiologically based climate response models.

## Ecological Models

There are several ecological models that can be used to assess sensitivity and vulnerability of important ecological processes to climate change. Ecological response models evaluate how climate change variables affect fundamental ecological processes such as carbon and nitrogen fluxes, evapotranspiration, and plant nutrient cycling (Christensen et al. 2008; Tague et al. 2009). The CENTURY model is a general model of plant–soil nutrient cycling and it has been used to simulate carbon and nutrient dynamics for different types of ecosystems, including grasslands, agricultural lands, forests, and savannas (Ojima et al. 1996). DayCent-Chem, which was built off of the CENTURY model, predicts carbon and nitrogen dynamics within forests and leaching of different types of nitrogen cations from the forests to streams (Hartman et al. 2007). The MC1 model is a dynamic vegetation model that combines the CENTURY biogeochemical model with a biogeographical model, MAPSS (Mapped Atmospheric-Plant Soil System) (Bachelet et al. 2001). The Regional Hydro-Ecologic Simulation System (RHESSys) is a GIS–based hydro-ecological modeling framework, which simulates how water, carbon, and nutrients fluctuate through the environment on a watershed scale (Christensen et al. 2008). The PnET is a suite of three nested computer models, which provide a modular approach to simulating the carbon, water, and nitrogen dynamics of forest ecosystems (Aber et al. 1995). All of these have climate-related inputs that permit an analysis of the potential impacts of climate change on fundamental ecological and hydrological processes.

Some of these models can be downloaded from the Internet, including RHESsys (http://fiesta.bren.ucsb.edu/~rhessys/), PnET (http://www.pnet.sr.unh.edu/), and the CENTURY model (http://www.nrel.colostate.edu/projects/century5/).

## Box 4.2. Ecological Thresholds

**Ecological thresholds** are important when considering response models because they represent situations where a small change in a driving variable, such as temperature or precipitation, leads to a disproportionately large response. When a system crosses such a threshold, the fundamental drivers and important processes can change abruptly, and these abrupt departures are often very difficult to include in models. In biological systems, climate-related threshold events include death of corals as a result of high water temperatures (Ward et al. 2007), widespread loss of piñon pines due to drought and high temperatures (Breshears et al. 2005), and the sudden eruption of spruce beetle in Alaskan forests when recent temperature increases permitted reproduction in a single season (Werner et al. 2006).

At the level of a single species, threshold events may result from a simple, direct effect of climate, such as exceeding a lethal temperature. At the ecosystem level, threshold events may be very broadly distributed, and they frequently involve positive feedbacks that amplify effects that otherwise may been a smaller perturbation to the system (U.S. CCSP 2009a). Wildfire behavior is a good example of a physical process with multiple thresholds (Peters et al. 2004). When small, wildfire spread is determined largely by local fuel attributes. As fire extent and intensity increase, several thresholds are crossed and the processes that drive fire behavior are almost completely different. Very large wildfires generate their own surface winds that can drive a fire across areas with small fuel loads and little fuel connectivity. Models with fundamentally different structures, scales, and processes are needed to accurately simulate wildfires across this range of scales (Peters et al. 2004).

Thresholds pose special problems for conducting climate change vulnerability and risk assessments. We know little about the location, even approximately, of most ecological thresholds, while the consequences of crossing a threshold can be profound. A commonsense approach to thresholds is to focus on an opposing attribute—the resilience of an ecological system. Resilience is the ability of a system to retain characteristic processes and structures when subjected to change or disturbance. As mentioned previously, many recommendations for responding to climate change focus on increasing the resilience of systems (U.S. CCSP 2009a; Heller and Zavaleta 2009), and these actions will help avoid catastrophic thresholds.

## Limitations of Response Models

All models are simplifications of the real world and, as such, have limitations in their use and applications. Most response models used in vulnerability assessments are simple models involving shifts in species ranges based on direct interactions with climate change (e.g., temperature tolerance), or based on shifts in habitats associated with climate change. These approaches are used because data on species attributes (e.g., demography, habitat preferences, etc.) and species and habitat distributions are available. However, these models tend to ignore other factors and species traits that can affect vulnerability to climate change. These include:

- Changes in interactions between species, including competitive interactions and disease (Peterson et al. 2002; Murray et al. 2006).

- Nonlinear, complex responses (e.g., thresholds or tipping points) associated with indirect interactions (Burkett et al. 2005) (see Box 4.2).

- Interactions between climate change and other important drivers or stressors such as land-use and land-cover change (Root and Schneider 2002).

- Horizontal flow processes such as species migration (immigration/emigration) that can determine a species' ability to move across an area, either in direct response to climate change or as an indirect response to habitat shifts (McRae et al. 2008).

Another issue regarding response models is transferability to different geographies and scales. General relationships established using broad-scale response models may not hold up when assessing vulnerability of a species at a local scale (Frederiksen et al. 2004; Torti and Dunn 2005). Moreover, it may be difficult to transfer response models developed in one biophysical setting to another because of differences in local responses to climate variables (Primack et al. 2009).

Species selection may also affect the outcome of vulnerability assessments. Species with limited distributions have greater uncertainty in their response to climate change than species with broader ranges (Schwartz et al. 2006). Therefore, decisions on which species to include in a vulnerability assessment can affect the outcome and accuracy of the assessment.

Potential responses of species to climate change also may be affected by landscape context. Landscape context has been shown to be an important factor in species survivorship and response to stressors such as land use (Ricketts 2001; Baum et al. 2004). Most species response models lack factors associated with landscape context and pattern. One exception is the PATCH model (Schumaker et al. 2004), which incorporates aspects of landscape pattern and species traits in assessing vulnerability. This model can be downloaded from the Internet (http://www.epa.gov/wed/pages/news/03June/schumaker.htm).

## Availability of Response Models

We highlighted a variety of models that can be downloaded from the Internet. Some of these models are relatively simple to use, while others require extensive data sets and adjustments to the models for individual applications. However, even simple models should be used carefully, with close examination of the caveats involved on any particular modeling approach. There is a need for a Web portal that provides links to the range of existing response models, and for enhanced simulation frameworks that facilitate linking (e.g., climate models to ecological response models). The Terrestrial Observation and Prediction System is an example of a sophisticated simulation framework that links historical climate data, remotely sensed data, climate projections, and response models (Nemani et al. 2009).