Global Change in Forests: Responses of Species, Communities, and Biomes

ANDREW J. HANSEN, RONALD P. NEILSON, VIRGINIA H. DALE, CURTIS H. FLATHER, LOUIS R. IVERSON, DAVID J. CURRIE, SARAH SHAFER, ROSAMONDE COOK, PATRICK J. BARTLEIN

Global change is often perceived as human-induced modifications in climate. Indeed, human activities have undeniably altered the atmosphere, and probably the climate as well (Watson et al. 1998). At the same time, most of the world's forests have also been extensively modified by human use of the land (Houghton 1994). Thus, climate and land use are two prongs of human-induced global change. The effect of these forces on forests is mediated by the organisms within forests. Consideration of climate, land use, and biological diversity is key to understanding forest response to global change.

Biological diversity refers to the variety of life at organizational levels from genotypes through biomes (Franklin 1993). The responses of ecological systems to global change reflect the organisms that are within them. While ecologists have sometimes not seen the forest for the trees, so to speak, it is also true that forests cannot be understood without knowledge of the trees and other component species. It is the responses of individual organisms that begin the cascade of ecological processes that are manifest as changes in system properties, some of which feed back to influence climate and land use (Figure 1). Beyond its role in ecosystems, biodiversity is invaluable to humans for foods, medicines, genetic information, recreation, and spiritual renewal (Pimentel et al. 1997). Thus, global changes that affect the distribution and abundance of organisms will affect future human well-being and land use, as well as, possibly, the climate.

INTERACTIONS BETWEEN CLIMATE CHANGE AND LAND USE ARE PROJECTED TO CAUSE LARGE SHIFTS IN BIODIVERSITY

This article serves as a primer on forest biodiversity as a key component of global change. We first synthesize current knowledge of interactions among climate, land use, and biodiversity. We then summarize the results of new analyses on the potential effects of human-induced climate change on forest biodiversity. Our models project how possible future climates may modify the distributions of environments required by various species, communities, and biomes. Current knowledge, models, and funding did not allow these analyses to examine the population processes (e.g., dispersal, regeneration) that would mediate the responses of organisms to environmental change. It was also not possible to model the important effects of land use, natural disturbance, and other factors on the response of biodiversity to climate change. Despite these limitations, the analyses discussed herein are among the most comprehensive projections of climate change effects on forest biodiversity yet conducted. We conclude with discussions of limitations, research needs, and strategies for coping with potential future global change.

Andrew J. Hansen (e-mail: hansen@.montana.edu) is an associate professor in the Ecology Department at Montana State University, Bozeman, MT 59717. Ronald P. Neilson is a bioclimatologist with the USDA Forest Service, 3200 S.W. Jefferson Way, Corvallis, Oregon 97331. Virginia H. Dale is a senior scientist in the Environmental Sciences Division at Oak Ridge National Laboratory, Oak Ridge, TN 37831. Curtis H. Flather is a research wildlife biologist, USDA Forest Service, Rocky Mountain Research Station, 2150 Center Ave., Bldg A, Fort Collins, CO 80526–1891. Louis Iverson is a research landscape ecologist with the USDA Forest Service, Northeastern Research Station, 359 Main Road, Delaware, OH 43066. David J. Currie is professor and chair of the Biology Department at the University of Ottawa, University of Ottawa, Box 450, Station A, Ottawa, Ontario, K1N 6N5. Sarah Shafer, now a research geologist with the US Geological Survey Earth Surface Team, Denver, CO 80225, was a research associate in the Department of Geography at the University of Oregon while this article was being prepared. Rosamonde Cook was a postdoctoral research associate in the Department of Fishery and Wildlife Biology at Colorado State University while this article was being prepared. Patrick J. Bartlein is a professor in the Department of Geography at University of Oregon, Eugene OR, 97403-1251. © 2001 American Institute of Biological Sciences.

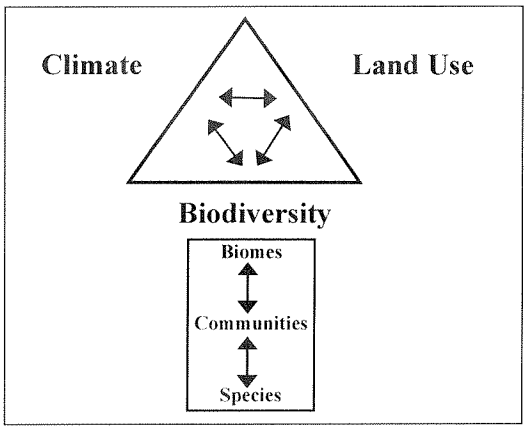

Figure 1. Conceptual model of the aspects of global change. Several other factors that may influence biodiversity are discussed in the text but are not included in the modeling of biodiversity response to climate change.

Effects of global change on species, communities, and biomes

This review focuses on three levels of biodiversity: species, communities, and biomes. Communities are assemblages of interacting species, such as spruce–fir forests or tallgrass prairies. Biomes are major biogeographic regions consisting of distinctive plant life forms (e.g., forests, grasslands). The distributions of species reflect their differential responses to climate, edaphic factors, and biotic interactions, such as competition and herbivory. These species dynamics provide the mechanisms by which communities and biomes respond to global change. At the same time, biomes and communities may constrain the nature of the species' response. For example, species may not be able to shift range without being accompanied by mutualists such as pollinators.

The distribution and abundance of a species are governed by the birth, growth, death, and dispersal rates of individuals comprising a population. These vital rates are, in turn, influenced by environmental factors, including climate, which alter resource availability, fecundity, and survivorship (Hansen and Rotella 1999). When aggregated across populations, changes in vital rates manifest as local extinction and colonization events, which are the mechanisms by which species' ranges change. Some of the best evidence that species' distributions are affected by changing climates is found among plants. The North American flora shifted during Holocene warming and the rates and direction of response differed among species (Webb 1992).

The birth, death, and other vital rates of species are also affected by land use. Humans modify the quality, amount, and spatial configuration of habitats. Degradation of habitat quality or quantity can reduce population size and growth rates and elevate the chance of local extinction events (Pulliam 1988). Such habitat loss can reduce genetic diversity, and the ability of species to evolve adaptations to new environments (Gilpin 1987). Land use may also alter the habitat spatial pattern, increasing the distances among habitat patches. An important consequence of this habitat fragmentation is a reduction in habitat connectivity, which could constrain the ability of many species to move across the landscape in response to climate change (Primack and Miao 1992, Iverson et al. 1999a).

Because of the individualistic responses of species, biotic communities are not expected to respond to climate change as intact units. Community composition will change in response to a complex set of factors, including the direct effects of climate, differential species dispersal, and indirect effects associated with changes in disturbance regimes, land use, and interspecific interactions (Peters 1992). Such an individualistic perspective implies that the impacts of climate change on communities can be understood by the aggregate response across species. However, this perspective may be flawed, because interactions among species are not yet sufficiently understood. An alternative view suggests that climate change may affect community-level characteristics, such as species richness and resilience to perturbation.

Climate may also influence community characteristics by altering the energy available to organisms. Wright et al. (1993) found that species richness is often related to ecological productivity, observing frequent correlations with climate, food availability, and limiting nutrients. These factors have all been interpreted to reflect energy availability in a system. Those areas receiving more energy often have a more complex partitioning of usable energy among species, and thus a greater richness, than those areas receiving less energy (Currie 1991). The influence of species richness on ecosystem function is complex. Ecosystems with higher native species richness are sometimes more resilient to perturbation (Frank and McNaughton 1991, but see also Wardle et al. 2000). Also, the presence of exotic species may elevate species richness but inhibit ecosystem function. Nonetheless, the diversity–resilience relationship may be important in anticipating ecosystem response to future climates.

Land-use activities also affect the availability of energy in ecosystems. Nearly 40% of the Earth's net primary productivity has been diverted to support human populations (Vitousek et al. 1986). This change in land cover has resulted in the conversion of native habitats supporting diverse species assemblages to intensive land uses that support only simplified, low-diversity communities (Rapport et al. 1985). The impacts of eroding biodiversity could include reductions in resilience, resistance to invasion, and ecological services provided to humans.

Climate is the primary force shaping the major biomes of the world. Mean and variation in annual precipitation and temperature explain much of the observed pattern of biome distribution (Prentice 1990). Shifts in biome location depend on the movements of key species. Because the predicted rates of climate change will push the climatic boundaries of biomes northward at a rate faster than the predicted rate of species migration (Davis and Zabinski 1992), shifts in biomes will probably lag behind changes in climate.

Land-use activities may appear to be too local in scale to affect regional biome distributions. However, in some biomes, such as the North American Prairie, land conversion is so extensive that little native vegetation remains. Land use can also affect biomes to an extent greater than the sum of the area directly affected. Conversion of natural vegetation to anthropogenic cover types can alter the frequency and scale of disturbance agents that also define the character of biomes. For example, fire suppression and grazing in the American Southwest are thought to be partially responsible for the invasion of woody vegetation into arid grassland habitats (Brown and Davis 1995). For a more compete discussion of interactions between climate change and disturbance, see Dale et al. (2001).

Feedbacks among climate, land use, and biodiversity

Climate and land use often interact in ways that influence biodiversity, implying that these factors cannot be considered in isolation. For example, land use may modify climatic impacts on species distributions by altering dispersal routes. Where land use creates barriers to dispersal for native species and facilitates dispersal for exotic species, climate change in human-dominated landscapes is likely to select for exotic species and against many native species (Malanson and Cairns 1997). Such constraints on dispersal are of concern especially around nature reserves. Organisms "trapped" in reserves by surrounding land use may become extinct if they are not able to disperse to increasingly suitable habitats in other nature reserves (Halpin 1997). Even in nature reserves, "weedy" species will most likely be quick to replace native species that succumb to climate change.

Climate and land use also jointly influence disturbances such as wildfire, flooding, and landslides. Some land uses preset the landscape to be very sensitive to extreme climate events, leading to severe disturbance. Logging can cause drying of fuels and allow severe fires during normal drought periods (Franklin and Forman 1987). This situation is thought to have transpired in Indonesia, where slash-and-burn agricultural practices provided fuels and ignition sources when an El Niño event induced drought in 1997. Consequently, vast areas of the rainforest burned, possibly jeopardizing many endemic species. Roads and logging practices can similarly increase land sliding and flooding during storm events (Swanson and Dryness 1975). Livestock grazing, on the other hand, often reduces fuel loads and reduces wildfire frequency and intensity for a given climate condition (Arno and Gruell 1983).

Changes in land-cover patterns can also directly affect climate, which in turn influences biodiversity (Dale 1997). For example, deforestation over large areas can cause reductions in transpiration, cloud formation and rainfall, and increased levels of drying (Dickenson 1991). Such changes can lead to dramatic shifts in biome type, such as the replacement of forests by shrubs or grassland. Similarly, agricultural land use and irrigation in the western Great Plains has been associated with increased cloudiness and precipitation in the Rocky Mountains of Colorado (Chase et al. 1999).

Recent responses of biodiversity to global change

Trends in biodiversity to changes in climate and land use over the last 100 years provide a context for understanding future interactions. During the past century, average air temperatures have increased 0–2 °C over most of the United States and Canada (Watson et al. 1998). Changes in precipitation have been variable over this period, increasing from 5% to 20% over most of the United States, but decreasing up to 20% in the Northern Rockies and California (Watson et al. 1998). The US population grew from 76 million in 1900 to over 270 million in 1998. Agricultural lands increased in area until 1900 then decreased slowly until 1950; they have remained stable since then (Maizel et al. 1999). Between 1942 and 1992, urban area increased 120%, while protected areas increased 80% (Flather et al. 1999). Rural residential development has increased rapidly in the mountain west in recent decades, expanding human influences into semi-natural habitats.

Many species and communities have responded to these changes in climate and land use. For example, forest decline and dieback are evident along the Atlantic and Pacific coasts and may be related to elevated CO_2 levels and climate change (Mueller-Dombois 1992). The breeding ranges of some mobile species, such as waterfowl, have been expanding northward in association with climate amelioration (Abraham and Jefferies 1997). Shifts in demography are apparent in some species. Both amphibians and birds in Great Britain have shifted breeding dates by 1 to 3 weeks earlier since the 1970s in association with increasing temperatures (Beebee 1995, Crick et al. 1997).

Species associated with human-dominated landscapes have greatly expanded in recent years. These include many large ungulate and small mammal species, waterfowl, and some bird species associated with agricultural and urban environments (Flather et al. 1999). Some of these species are now so abundant (e.g., deer) that the primary concern is controlling their populations. Many exotic species have also become established in the United States and greatly expanded their ranges (Drake et al. 1989).

At the same time, several natural community types and numerous species have been greatly reduced by human activities. For example, natural spruce–fir, longleaf pine, and loblolly–shortleaf pine forests now cover less than 2% of their presettlement ranges (Noss et al. 1994) and are likely to be further reduced under global warming. Many species dependent upon these endangered and reduced ecosystems are currently in peril. The number of species listed as threatened and endangered in the United States under the Endangered Species Act currently totals 1232 (USDI 2000). Factors contributing to species endangerment include habitat conversion, resource extraction, and exotic species (Wilcove et al. 1998). The spatial distribution of such factors results in

Table 1. General circulation models and predictions for change from current average annual temperature (dT) and precipitation (dP) for the coterminous United States under a doubling of atmospheric CO_2. The equilibrium-type models simulate an instantaneous increase in CO_2 and are run until equilibrium climate conditions emerge. The newer transient models assume trace gases increase at 1% per year until 2100, and allow the climate to adjust while incorporating inherent lags in the ocean–atmosphere systems. The HADCM2SUL and CGCM1 scenarios include the effects of sulfate aerosols. The dT and dP values from the transient scenarios were calculated from averages of the last 30 years of the scenarios compared with the 1961–1990 means.

Name	Acronym	Type	Reference	dT (°C)	dP (%)
Oregon State University	OSU	Equilibrium	Schlesinger and Zhao 1989	3	2.1
Geophysical Fluids Dynamics Laboratory	GFDLR30	Equilibrium	Manabe et al. 1990	4.2	18.9
Goddard Institute for Space Studies	GISS	Equilibrium	Hansen et al. 1988	4.4	5.1
United Kingdom Meteorological Office	UKMO	Equilibrium	Wilson and Mitchell 1987	6.6	11.3
UKMO Hadley Centre	HADCM2SUL	Transient	Johns et al. 1997	2.8	22.9
UKMO Hadley Centre	HADCM2GHG	Transient	Johns et al. 1997	3.7	30.7
Canadian Climate Centre	CGCM1	Transient	Boer et al. 2000	5.2	21.5

species at risk being concentrated in particular regions of the United States, especially the southern Appalachians, the arid Southwest, and coastal areas (Flather et al. 1998).

Biodiversity under future global change

Given past relationships among climate, land use, and biodiversity, how might biodiversity respond to future global change? We assess potential vegetation response to projected future climate change for doubled CO_2 concentrations by using the climate predictions of general circulation models (GCMs) (Table 1) as input to a set of different vegetation simulation models. The primary focus is on the potential continental-scale response of forest vegetation as reflected in changes in the distributions of biomes, community types, and tree species. Although vegetation models incorporating land-use dynamics are under rapid development at local scales, the current state of knowledge does not allow for integrating the effects of land use at the continental scale. In our assessment, we chose to emphasize forests as a key element of biodiversity, which allowed us to draw implications for other organisms that require forest habitats. We also simulate changes in species richness of trees and terrestrial vertebrates based on energy theory (Currie 1991) and examine potential effects of climate change on locations where endangered species are concentrated. Results are for the coterminous United States, unless stated otherwise. Each of these assessments is summarized here and reported in detail elsewhere (Table 2).

The models used to anticipate biodiversity responses to changes in climate are based on empirical relationships between organisms (vegetation and animals) and the environments they currently occupy. By using these relationships to predict biodiversity response, we are implicitly assuming that these environment–organism relationships will remain unaltered in the future. Although this approach can be criticized for not modeling some or all of the actual mechanisms leading to shifts in vegetation and species ranges, such an approach is commonly taken (Rogers and Randolph 2000) to initially assess ecological responses to global change scenarios. It is also important to emphasize that the given GCMs are coarse-grid, regionally smoothed outputs that do not allow depiction of local or even subregional climates. Consequently, the vegetation outputs modeled here must also be considered coarse and not sensitive to local phenomena.

Climate change scenarios. The GCMs differ in formulation, hence predictions vary among the models. Consequently, the simulations are best considered as possible alternative views of the future, with unknown likelihood of occurrence. Both equilibrium and transient GCM scenarios are used in this assessment to incorporate a broad array of possible futures (see Aber et al. 2001). We put greater confidence into outcomes for which the models are in agreement; we take disagreement among the models as an indication of uncertainty. Thus, we report major findings for which most of the models agree and we point out disagreement. Still, the uncertainty level for each climate and vegetation output is unknown, and probably high, given the uncertainty in forecasting climate and subsequent vegetation responses.

For the coterminous United States, the different climate scenarios all predict some level of warming and increased annual precipitation (Table 1). Mean annual temperature increases vary from 3.3°C to 5.8°C, with the greatest warming at higher latitudes. Mean annual precipitation is predicted to increase

Table 2. Biodiversity models used in this analysis.

Response variables	Model	Model type	Resolution	Extent	GCMs simulated	Reference
Biomes, community types	MAPSS	Biogeographic processes	10 km grid	coterminous United States	HADCM2S, HADCM2G, CGCM1, OSU, GFDL–R30, GISS, UKMO	Neilson 1995, Bachelet et al. 2001
Tree species, forest community types	DISTRIB	Statistical regression tree	County	Eastern United States	HADCM2S, CGCM1, GFDL–R30, GISS, UKMO	Iverson and Prasad 1998, 2001
Tree and shrub species	Response surface model	Statistical local regression	25 km grid	North America	HADCM2S, CGCM1	Shafer et al. 2001
Species richness of trees, mammals, birds, reptiles, amphibians	Currie model	Statistical	2.5° x 2.5° lat and long south of 50°N; 5° long x 2.5° lat north of 50°N	United States and Canada	CGCM1, OSU, GFDL–R30, GISS, UKMO	Currie 2001

in the West, with 20% to more than 50% increases in California. Decreased precipitation of up to 30% is predicted for locations in the Southeast, Texas, and the Northwest.

Biomes. The MAPSS biogeography model (Neilson 1995) projects biome response to climate as change in vegetation structure and density based on light, water, and nutrient limitations (VEMAP members 1995, Bachelet et al. 2001). Vegetation is coupled directly to climate and hydrology, and rules are applied to classify vegetation into biome types. The model considers the effects of altered CO_2 on plant physiology. MAPSS simulates potential natural vegetation (specifically, life-forms) based on climate and does not include succession or plant dispersal.

The results project that potential forest area decreases by an average of 11% across the GCM scenarios, with a range of +23% under the coolest scenarios and –45% under the hottest scenarios (Figure 2). Northeast mixed (hardwood and conifer) forests decrease by 72% in potential area, on average (range –14% to –97%), as they shift into Canada and increase in potential area continentally (Watson et al. 1998). The potential area of eastern hardwoods decreases by an average of 34% (range –93% to +51%). These deciduous forests shift north, replacing northeastern mixed forests, but are squeezed from the south by southeastern mixed forests or from the west by savannas and grasslands, depending on the scenario. The potential range of southeastern mixed forests increases under all scenarios (average 37%, range 25% to 57%) while shifting north. This biome remains intact under cooler scenarios but is converted to savannas and grasslands in the South under the hotter scenarios.

Potential environments for alpine ecosystems all but disappear from the western mountains, being overtaken by encroaching forests. Wet coniferous forests in the Northwest decrease in potential area by 9% on average (range –54% to +21%). The potential range of interior western pines change little on average, with a range of –30% to +39%. The potential range of shrublands and arid woodlands expand in the interior West and Great Plains, encroaching on some grasslands. However, grassland habitats may expand in the deserts of the Southwest, parts of the Southeast, and possibly in the upper Midwest. Thus, the potential area of grassland could either decrease or increase.

The projections agree on a single or on two vegetation classes across 68% of the coterminous United States. Locations of greatest certainty are in the northern plains and Florida. Regions of great uncertainty are transition zones in the eastern prairie and the West. Taken in order of increasing temperature change, the future scenarios imply that potential forest range could expand with small amounts of warming but would contract under the hotter scenarios.

Forest community types and tree species. Statistical models are used to project the distributions of tree species, with results aggregated into community types. These models project tree response to future climate, based on current relationships between trees and environmental variables such as climate and soils. Because physiological data are not required (as is the case for process models), many species can be modeled. However, these approaches do not include important forest dynamics involving species interactions, physiological processes such as CO_2 uptake, and tree dispersal and establishment. They also assume that species–environment relationships will remain the same under future climate conditions, which may not be the case.

Two statistical models are used. The DISTRIB model of Iverson and Prasad (Iverson and Prasad 1998, Iverson et al. 1999a, Prasad and Iverson 1999) was applied to the eastern United States. This model uses regression tree analysis, based on 33 environmental variables, to predict the potential future distribution of suitable habitat for 80 tree species. An index of species response (regional importance) was

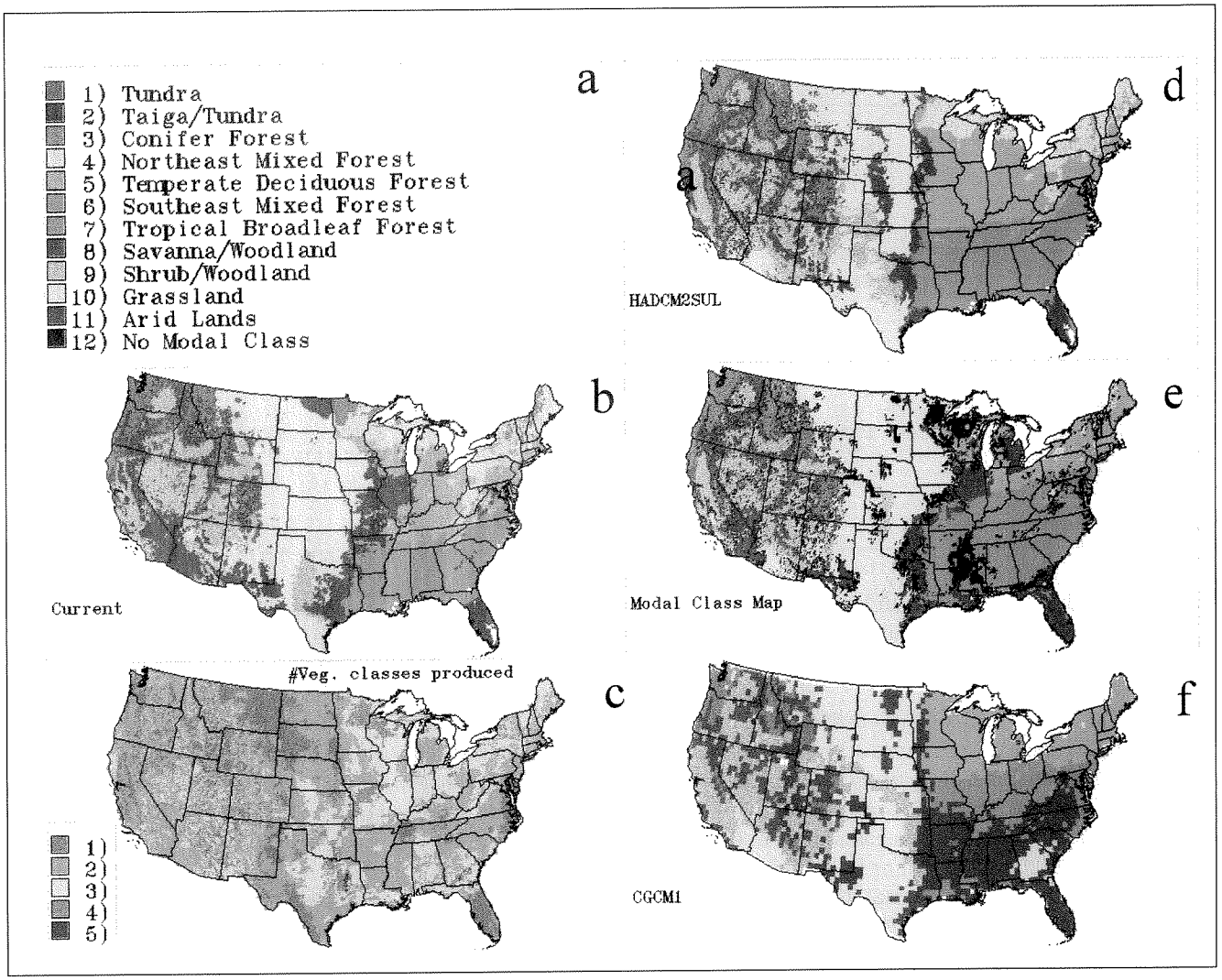

Figure 2. Simulated potential distributions of biomes, using the MAPSS biogeography model under six different GCM scenarios representing approximately 2 × CO_2 concentration. (a) Color key for biomes; (b) simulated current biome distribution based on average (1961–1990) climate; (c) uncertainty map (the number of unique biome types simulated across all six GCM scenarios are plotted); (d) biome distribution under the HADCM2SUL scenario, among the coolest of future warming scenarios; (e) a modal map of future biome distributions (shown are the biomes most often simulated for the future across all six GCMs; refer to panel c for the "uncertainty" associated with the modal map); (f) biome distribution under the CGCM1 scenario, among the warmest of future scenarios.

derived by multiplying the importance value (reflecting the relative abundance of a species in a community) by the area for each county. Community types were then defined by simply aggregating the importance values for individual tree species (Iverson and Prasad 2001). For western forests, we drew on the work of Shafer et al. (2001) and Bartlein et al. (1997), who use a local regression model to predict probability of occurrence of tree species across North America based on climate and soils. The results for dominant western species are presented.

In the eastern United States, the area of habitat suitable for oak–hickory expands in area following climate change by an average of 34%, primarily to the north and east (Figure 3). The oak–pine habitat also expands by roughly 290% and is represented throughout the Southeast. On the other hand, the habitat capable of supporting the spruce–fir and aspen–birch types are dramatically reduced (–97% and –92%) and are largely replaced by oak–hickory and oak–pine habitat. The loblolly–shortleaf pine habitat is also reduced by 32%; it shifts to the north and west while being replaced in its current zone by oak–pine habitat. The longleaf–slash pine habitat is reduced, on average, by 31%. There is a higher level of disagreement among climate scenarios for the elm–ash–cottonwood, oak–gum–cypress, and white–red–jack pine types, which show increases in habitat under some scenarios and decreases under others.

These potential changes in habitat for community types reflect the responses of individual tree species. Seven of the 80 species modeled were predicted to have their suitable habitat reduced in regional importance by at least 90%: bigtooth

aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), sugar maple (*Acer saccharum*), northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), red pine (*Pinus resinosa*), and paper birch (*Betula papyrifera*). An additional 24 species would potentially decline by at least 10%. In contrast, regional importance increased for 35 species, including 12 species that increased suitable habitat by 100% or more, including four species of oak and one hickory.

Most species' habitat was projected to move to the north, 100 to 530 km for several species. Some species, such as quaking aspen, paper birch, northern white cedar, balsam fir, and sugar maple have the optimum latitude of suitable habitat move north of the US border.

All of the above analyses for the eastern United States relate to the potential distribution of suitable habitat, not actual distribution of the species. The assumption is that the species will get there, that there are no barriers or constraints to migration. (For newer projections that consider dispersal, see Iverson et al. 1999b).

In the western United States, the potential ranges of dominant rainforest conifers such as western hemlock are projected to decrease west of the Cascade Mountains and expand into mountain ranges throughout the interior West. Simulated potential habitat for Douglas fir (*Pseudotsuga menziesii*) also decreases along the western coast of the coterminous United States but expands east of the Cascades and Sierras as

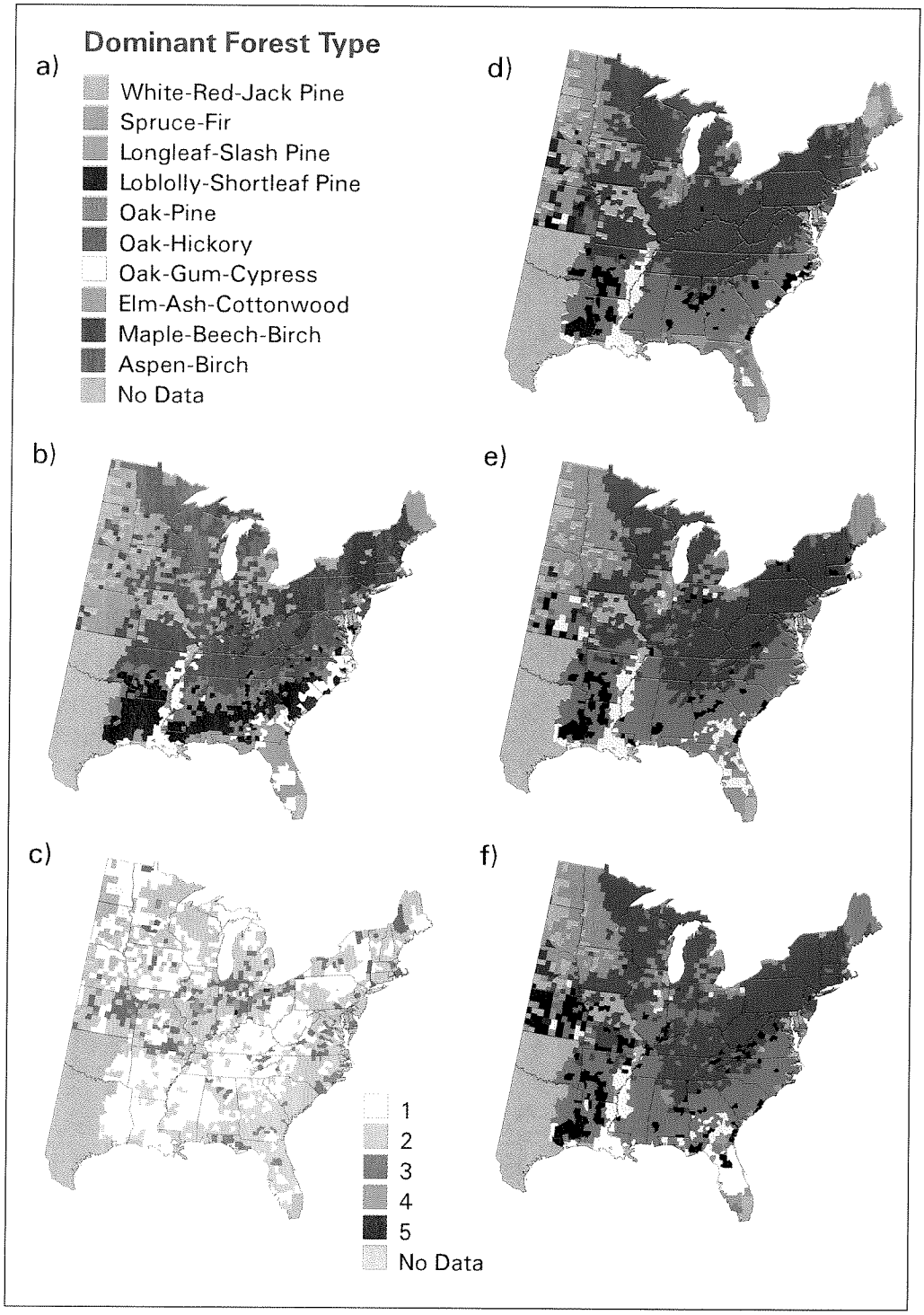

Figure 3. Simulated potential distributions of forest community types in the eastern United States using the DISTRIB model under five different GMC scenarios representing approximately 2 x CO_2 concentration. (a) Color key for forest types; (b) current forest type distribution based on 100,00 actual forest inventory plots; (c) uncertainty map (plotted are the number of unique forest community types simulated across all five future GCM scenarios); (d) potential forest community type distribution under the HADCM2SUL scenario, among the coolest of future warming scenarios; (e) a modal map of future biome distributions (shown are the biomes most often simulated for the future across all five GMCs; refer to panel [c] for the "uncertainty" associated with the modal map); and (f) forest community type distribution under the CGCM1 scenario, among the warmest of future scenarios.

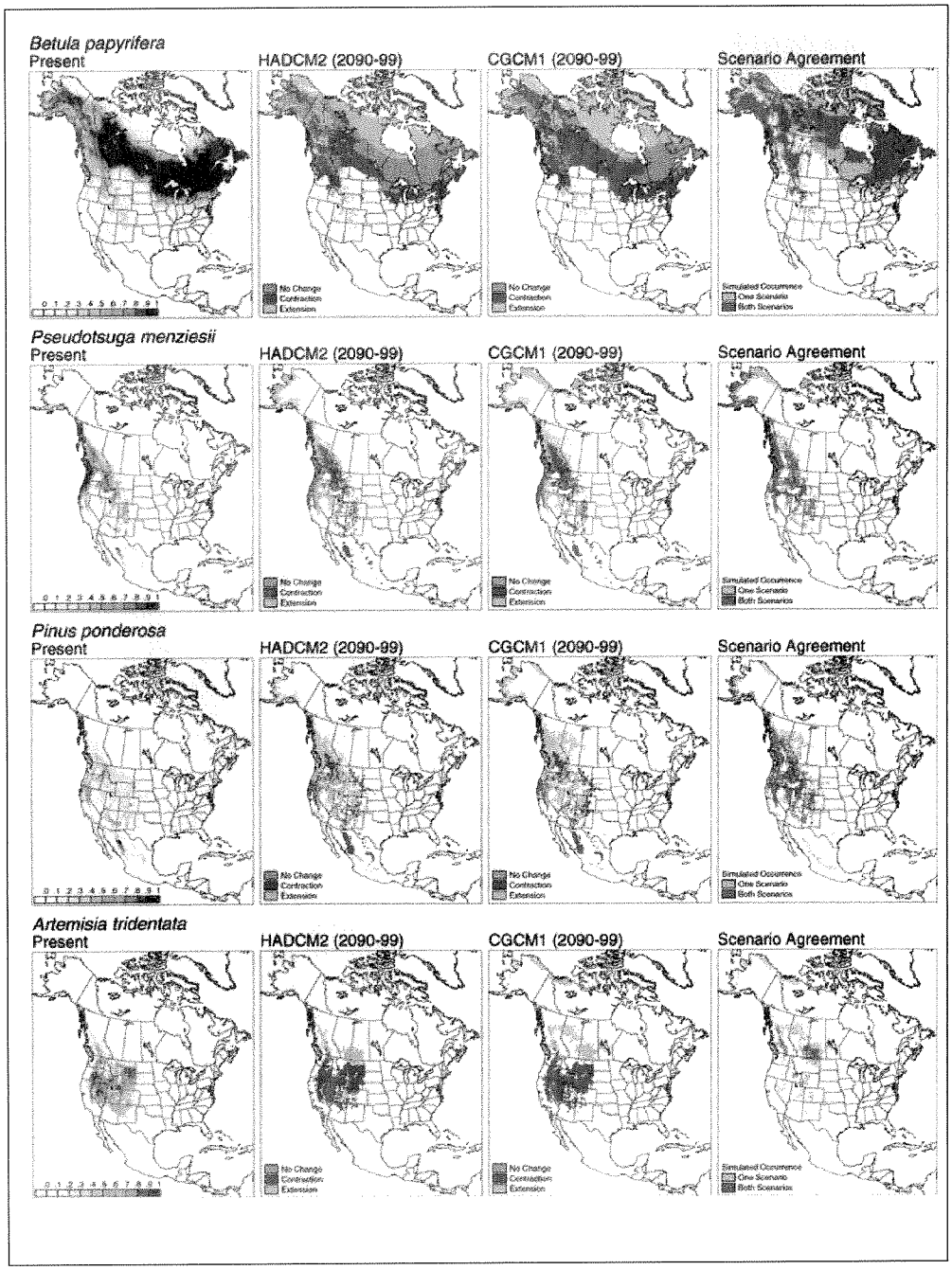

Figure 4. Simulated distributions and scenario agreement for **Betula papyrifera, Pseudotsuga menziesii, Pinus ponderosa,** *and* **Artemisia tridentata.** ***Estimated probabilities of occurrence for a taxon simulated with observed modern climate (left panel). Comparison of the observed distributions with the simulated distributions under future climate conditions as generated by HADCM2S and CGCM1 for 2090–2099 (middle panels). Gray indicates locations where the taxon is observed today and is simulated to occur under future climate conditions; red indicates locations where the taxon is observed today but is simulated to be absent under future climate conditions; and blue indicates locations where the taxon is absent today but is simulated to occur under future climate conditions. Scenario agreement (right panel): Light purple indicates locations where the species is simulated to be present under the future climate of either the HADCM2S or CGCM1 scenario; dark purple indicates locations where the species is simulated to be present under both future climate scenarios.***

well as northward along the west coast of Canada into Alaska (Figure 4).

The potential range of several subalpine conifers is simulated to contract substantially in the western coterminous United States, including Englemann spruce (*Picea engelmannii*), mountain hemlock (*Tsuga mertensiana*), and several species of true fir (*Abies*). Potential ranges for these subalpine species are simulated to expand along the western coast of Canada and into Alaska. Potential future habitat for big sagebrush (*Artemisia tridentata*), an important shrub in the inland West, is largely absent in the United States, shifting into Canada. This shrub is simulated to be replaced in the United States by shrubs, chaparral, and grasslands, now found in arid regions of the Southwest. Potential habitat for ponderosa pine (*Pinus ponderosa*) is simulated to expand in the western United States, including on the West Coast, where many other conifers are projected to contract.

While the potential ranges of many taxa in the West shift northward, the topographic complexity of the region creates less intuitive changes in some species distributions. Potential habitat for some conifer species associated with mesic climates shifts south and east along the Rocky Mountains with, for example, forests typical today of Glacier National Park becoming dominant in Yellowstone National Park to the southeast (Bartlein et al. 1997). The direction of change may also differ from east to west within a species' range. Potential habitat for paper birch, whose range spans the continent, is simulated to contract northward in the eastern

United States but to expand southward along the Rocky Mountains in the West (Figure 4). The complex topography of the West results in simulated future habitat for many tree species that is disjunct. Consequently, dispersal to new habitats under climate change may be more difficult in the West than in the East, where the future distributions of species are simulated to be more continuous.

Community richness. Currie (2001) derived multiple regression models relating the broad-scale variability of species richness of trees and terrestrial vertebrates across North America to the spatial patterns of summer and winter precipitation and temperature. These models were used to predict patterns of species richness under five GCM scenarios. This approach assumes that richness will continue to covary with climate in the future in the same way that it does today.

The results indicate that contemporary patterns of richness correlate strongly with temperature and less strongly with precipitation. These climate-richness relationships differ among taxonomic groups; thus, projected change in richness under climate change also differed among groups. Current tree species richness is a positive function of temperature up to relatively high temperatures, then is negatively related to further increases in temperature. Current tree species richness is also a positive function of precipitation. Thus, climatic warming is predicted to lead to increased tree richness over most of the northern United States, especially in the areas that are now coldest: in the western mountains and near the Canadian Border (Figure 5). Moderate decreases in richness (–20%) are predicted to occur in areas that are likely to experience drying and very high temperatures, such as the southwestern deserts. The greatest disagreement among the projections was for Pacific Northwest. All models predict increases in richness in that area, but these increases may be modest (< +50%) to pronounced (> +100%).

Contemporary species richness of endotherms (birds and mammals) covaries strongly with temperature. Richness in these groups is maximal in moderately warm areas (the southern Appalachians and southern Rockies), and it decreases in hotter areas. This relationship may occur because ambient heat serves as a direct energy subsidy for endotherms in cold climates, but these organisms expend energy to dissipate heat in hot areas. Endotherm richness is only weakly related to precipitation. Consequently, under most climate change scenarios, endotherm richness is predicted to decrease by over 25% in low-elevation areas in the Southeast. Increases in richness (> +11% to > +100%), are predicted for upper montane areas across the United States.

Contemporary ectotherm (reptiles and amphibians) richness is even more strongly related to temperature, increasing monotonically as temperature increases. Ambient heat is also an energy subsidy for ectotherms, even in the warmest areas of the earth. Consequently, climatic warming is predicted to increase ectotherm richness over the entire coterminous United States. For reptiles, the increase is predicted to be modest across the South and greater in the North. Amphibian richness, in contrast, also depends somewhat on precipitation. Because most GCMs predict that the southeastern United States will become somewhat drier in winter, amphibian richness in the Southeast is predicted to change little despite increased temperatures, and to increase elsewhere. Differences among predictions of different GCMs lie mainly in how dramatically richness is likely to increase.

Threatened and endangered species. How might the changes in species richness predicted above influence endangered species hotspots (places where many endangered species occur)? We overlaid the maps of projected species richness over maps of current hotspots for threatened and endangered species (Flather et al. 1998) to determine the proportion of each endangerment hotspot area in the contiguous United States that is predicted to show an increase, decrease, or no change in species richness for each taxonomic group. The results indicated that reptiles and amphibians are expected to increase in richness across all endangerment hotspots. On the other hand, bird and mammal richness may undergo significant reductions in many endangerment hotspots, especially in the East (Figure 6).

Implications of assessment results

In contrast to public perceptions of large-scale forest loss under global change, the biome models project only a modest average loss of forest area (11%) for the coterminous United States. Lost forest is largely replaced by savanna and arid woodland biome types. However, the projected response of forest habitats to global change scenarios is highly variable among GCMs. Forest habitats are projected to increase by 23% under the HADCM2SUL model and are predicted to decrease by 45% under the UKMO model. This uncertainty points to cautious interpretation of our findings and to the need for further research directed at understanding the factors driving change in forest systems.

Within the climate projections considered, we did observe some common patterns in the response of forest community types across the continent. Areal expansion of habitats was projected for oak–hickory and oak–pine in the East and ponderosa pine and arid-tolerant hardwoods in the West. The first three of these are extremely valuable for forest products and as habitat. The heavy mast production of oak–hickory, for example, is a food source for more than 180 different kinds of vertebrates (Rogers 1990). The oak types also produce persistent coarse woody debris that benefits several ecological processes and organisms.

Suitable habitats for several important community types, however, are projected to greatly decrease in area or disappear from the coterminous United States. These include alpine habitats, subalpine spruce–fir forests, aspen, the maple–beech–birch type, sagebrush, and loblolly–shortleaf pine communities. Subalpine spruce–fir has been decreasing in area, becoming increasingly fragmented, and losing species richness since the last glacial period (Brown and Davis 1995). Other habitats such as sagebrush and aspen are being reduced in mod-

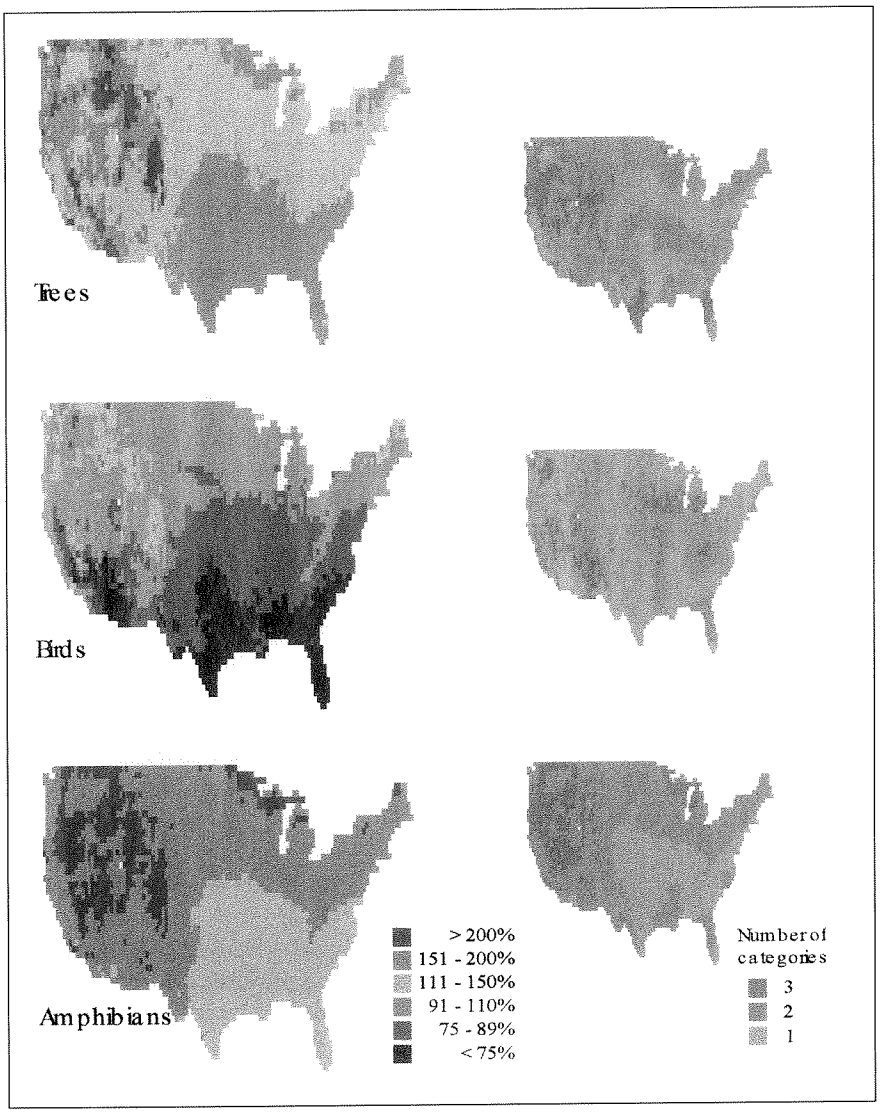

Figure 5. Predicted changes in species richness for trees (top left panel), birds (middle left), and amphibians (bottom left) after climate change, relative to current species richness. The predictions represent the mean richness predicted by five different GCMs. Maps of uncertainty (on the right) represent the extent of disagreement among GCMs. The number of different classes of richness (among those used in the figures on the left) predicted by the five different GCMs is shown. Thus, in areas represented in blue (one class), all GCMs lead to the same predicted change in richness, whereas in ocher-colored areas, three or more of the GCMs predicted changes that fell in different classes.

ern times by conifer encroachment, grazing, and exurban development. Climate warming is projected to further reduce these community types and the multitude of species dependent upon them. Quaking aspen, for example, is a keystone species in the west, where it is often the only abundant hardwood among the conifer forests. Its palatability, soft wood, and rapid decomposition result in many species of plants and animals being dependent upon it. Subalpine spruce–fir now supports several species that require wilderness conditions (e.g., wolverine, *Gulo luscus*). Sagebrush has several obligate species of vertebrates. The maple–beech–birch type includes several important tree species, such as red maple (*Acer rubrus*), sugar maple, black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). Reductions of these species will influence many associated organisms.

Suitable habitats for the forest types projected to decrease in the coterminous United States are generally expected to increase in Canada. Some of these northerly locations are underlain by permafrost and have nutrient-poor soils. More work is needed to determine which species could tolerate future conditions in the northern ecosystems. Important policy questions arise from the cross-border migration of species and ecosystems that are increasingly threatened in the United States but increasingly common in Canada. Such changes might suggest that the current national regulations and incentives on biodiversity be supplemented with international regulations and incentives.

Our projections of species richness based on energy theory suggest that climate change will favor greater tree species richness over much of the coterminous United States. Climatic conditions are also projected to become more favorable for amphibians and reptiles. Whether these climate changes will counter the current decline in amphibians caused by pollution, ultraviolet radiation, land use, and other factors will require further study. Climate conditions are predicted to lead to lower bird and mammal richness across the southern United States. What are the implications of this projection for the many bird species that winter in the southern United States and breed to the north? Perhaps of greatest concern are currently threatened or endangered bird and mammal species that are restricted to endangerment hotspots in the Southeast. The projected losses of species richness here could further imperil these populations. Individual species studies will be needed to begin to understand the implications of these changes.

These projections for species richness raise interesting questions for management. If climate change increases the potential for amphibian and reptile species richness, which species are likely to disperse to the newly suitable locations (Figure 7)? Are there opportunities to introduce desirable species to the newly suitable habitats and select against nondesirable species that are good dispersers? The projections for birds and mammals indicate no change or slight increases in

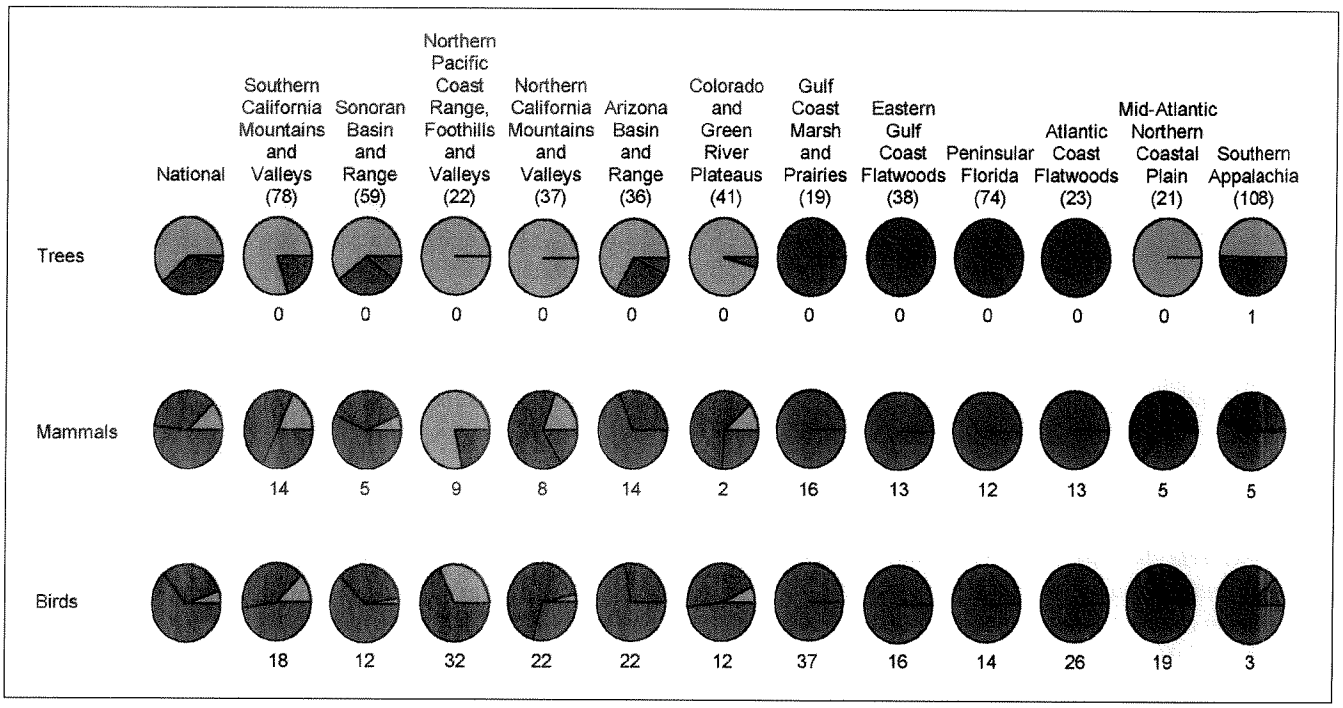

Figure 6. Proportion of hotspot areas that are predicted to lose (blue), gain (orange), or show no change (green) in species richness by taxonomic group. The numbers below hotspot names indicate the number of threatened and endangered species occurring in that hotspot. The numbers below the pie charts refer to the proportion of species for a given taxon (as defined by the row) in the hotspot (defined by the column). The results indicated that reptiles and amphibians are expected to increase in richness across all endangerment hotspots, hence data are not shown for these groups.

richness in the North, but decreases in the South. Which species in the southern areas are most likely to go extinct? Can management strategies be used to buffer these losses?

Limitations and caveats

The projections described above reflect the assumptions and formulations of our models. The results indicate potential trends in biodiversity if environment–organism relationships remain unchanged in the future, and if organisms do not encounter constraints that limit their ability to track climate changes. It is important to keep in mind the factors that may modify the relationship among climate and biomes, communities, and species.

Our approach was to project change in suitable habitats for various levels of biodiversity under the climate projections of several GCMs. Again, we emphasize that the accuracy of the climate projections is unknown. Our biodiversity models also add an unknown level of uncertainty to our projections of habitat change. Also, the climate and biodiversity models were done on relatively coarse spatial resolutions. Local variation in climate due to topography or other factors could result in species or communities being able to persist in suitable microhabitats, even though the coarser-resolution models project no suitable habitats in the location. Another assumption of our approach is that the current locations of species, communities, and biomes reflect environmental conditions suitable for all life-history stages of these organisms. In reality, however, the habitat requirements for seedling establishment may not be identical to those for the survival and reproduction of adult trees and shrubs.

The likelihood that organisms will be able to disperse to newly suitable habitats will vary considerably among species. Thus, differential rates of species dispersal will be a key determinant of future biodiversity patterns. During the Holocene, dominant plant species migrated at rates that allowed them to keep pace with climate change (Davis 1989). However, the estimated rates of dispersal during the Holocene, about 10–45 km per century (Davis and Zabinski 1992), were much slower than the potential geographic shifts implied by our analysis of forest communities. It is unclear how fast organisms may disperse in modern landscapes subjected to various levels and types of land uses. It is likely that dispersal rates will be slower than the rate of climate change and that weedy species will be better able than many other species to disperse through human-dominated landscapes.

These differential rates of dispersal suggest that actual plant communities under climate change will not resemble those predicted based on community–environment relationships. Instead, the new communities will initially be dominated by the subset of species (especially weeds) that are best able to track climate change. Complex vegetation dynamics should then follow as better competitors gradually arrive at these sites. Adding to the complexity are the dynamics of the species that occupied the site under previous climatic

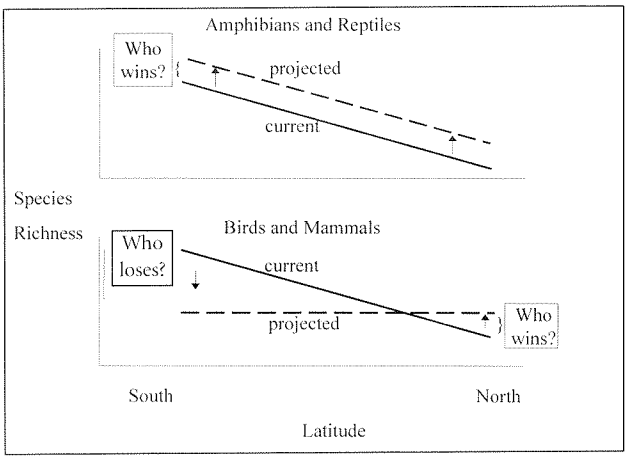

Figure 7. Current trends in species richness along a latitudinal gradient and projected trends under climate change (Currie 2001) for amphibians and reptiles and for birds and mammals. Projected increases and decreases in richness raise the question of which species will expand into newly suitable habitat and which species will go extinct in increasingly unsuitable habitat.

conditions. While some species are likely to vacate unsuitable sites rather quickly, others may persist for decades to centuries. Franklin et al. (1992) suggested that adult trees in old-growth forests in the Pacific Northwest may persist long after changing climate no longer allows regeneration. These forests could then change quickly as senescence or disturbance clears the site, allowing emigrating species to establish.

A final caveat on the projections is that they do not consider land use, disturbance, or fine-scaled vegetation dynamics (see Dale et al. 2001). Some community types, such as prairie and coastal chaparral, are now dominated by intense human land use, which has altered the expected pattern of disturbance and negatively influenced native species. Of the 63 factors that have contributed to species endangerment in the United States, land-use intensification associated with residential and urban development, forest management, grazing, and environmental contamination are the most common factors cited in nine out of the 12 endangerment hotspots (Flather et al. 1998). As the population of the United States increases, the area of seminatural habitats will be further reduced, causing deviations from the relationship between climate and biodiversity.

This list of limitations makes evident the complexity of the interaction of global change and biodiversity. Although it is important for researchers to attempt to predict future global change and consequences for biodiversity, society needs to be aware that the accuracy of these predictions may be mixed. The complex suite of interactions initiated by climate change could well lead to some unexpected outcomes. How to cope with such surprises may be one of the greatest challenges of future global change.

Coping strategies

Managing global climate-change impacts on biodiversity involves avoidance of impending climate and land-use changes, altering those changes, or accepting the changes and dealing with their impacts. Strategies to slow global change include reducing the atmospheric concentration of greenhouse gases, human-induced disturbances, and land-cover changes. Control of greenhouse gas emissions requires reduced use of fossil fuels and less harvesting of large trees for short-turnover products, as well as the establishment of new locations or means of carbon storage by such actions as planting large areas with rapidly growing trees or enhancing their carbon sequestration potential. However, carbon storage in large plantations of monocultures of nonnative species would jeopardize native diversity if those species replace natural vegetation. Strategies for reducing changes in land cover and use include management of human population growth, land-use planning, and land-use regulation and incentives programs. These strategies can be designed to foster biodiversity, if that goal is included in the overall plan.

Where the maintenance of ecosystem processes and native species is a priority, effective strategies may differ with location, community type, and management objective. For communities that are unlikely to migrate to suitable environments elsewhere (e.g., subalpine and alpine communities), it may be appropriate to minimize change by manipulating vegetation structure, composition, or disturbance regimes to favor the current community. For communities that may be able to reach newly suitable habitats, a reasonable strategy may be to manage some of the current habitat as a reservoir until the community is reestablished in the new locations. Other portions of the current habitat may be managed to encourage change to the new species and communities more appropriate for the new environment. Global change could offer opportunities to restore communities that are now degraded. In this case, management to induce rapid change may allow for the establishment of species deemed to be desirable by society.

In some cases diversity can be preserved only through reserves set aside to protect species in the face of global land changes. Halpin (1997) offers a strategic framework of this type for nature reserves. The framework involves both maintaining current communities and facilitating natural dispersal of organisms across elevational and latitudinal gradients (e.g., via migration or dispersal corridors). The five categories of management prescriptions presented by Halpin are (1) selection of redundant reserves, (2) selection of reserves that provide habitat diversity, (3) management for buffer-zone flexibility, (4) management for landscape connectivity, and (5) management for habitat maintenance. The exact prescription will vary, depending on characteristics of the species and communities to be preserved and their habitats. For the species most at risk, seed banks and captive breeding and rearing approaches may be necessary until new suitable habitats develop.

Much work is needed on methods to execute and evaluate such strategies. Simulation models and other decision-support tools are needed to assess the likely response of a community to global change and to evaluate the potential success of alternative management strategies. It is especially important that these models integrate consideration of climate, land use, and biodiversity. Adequate monitoring protocols are needed to establish rates of change in environmental drivers and species and community responses to these changes. Adaptive management experiments can be used to evaluate the success of management manipulations. These experiments should include manipulations of species distributions and performance through planting and release projects, habitat modification, genetic engineering, and eradication of undesirable species. In addition, species banks or refuges for colonization can be developed.

Decisions on mitigation of the effects of climate change on biodiversity involve social, political, and economic considerations. Therefore, these decisions will not be made solely within the ecological context of the issues. Instead, the full set of advantages and disadvantages of all decisions must be considered. However, choosing not to control greenhouse gases or not to manage species, communities, and landscapes in the face of climate change is making a decision about the impact of these changes on biodiversity. Rather than letting inaction decide the result of potential changes, active assessment and management will be necessary to bring the landscape to a state of desired future biodiversity conditions in the face of global climate change.

Research needs

As is apparent from the discussion above, aspects of global change research have substantial levels of uncertainty. Although considerable progress has been made toward understanding global change, major research initiatives will be required to reduce current uncertainty.

Future climate and land use. The predictions of current GCMs disagree to varying degrees and their levels of accuracy are not well quantified. The models could be better validated relative to past conditions at local to regional scales. This would allow research and management to focus on the future climate scenarios that are most plausible. In contrast to climate, relatively little effort has gone into understanding and predicting land-use and land-cover change. Studies are needed to project land cover and use based on biophysical factors and socioeconomic factors. Moreover, integrated models of climate and land use are needed to better predict future interactions between these two aspects of global change.

Tolerances of organisms. Much is known about the tolerances of some trees to climate, soils, and other biophysical controls. However, such knowledge is mostly lacking for other plants, vertebrates, and invertebrates. Similarly, little is known about the demographic performance of organisms across gradients in climate and land use (Hansen and Rotella forthcoming). This deficiency is especially apparent for population dispersal. Species at higher trophic levels will probably be more difficult to model under global change because they respond directly to climate as well as indirectly to the secondary effects mediated by habitat structure, ecological productivity, and interactions with other species. Thus, holistic examinations of species and environmental relationships are needed that consider multiple stressors and multiple spatial and temporal scales.

Biodiversity feedbacks. We emphasize that organisms mediate the effects of global change on ecosystems and feedbacks to climate and land use. What might be the consequences on the services provided by ecosystems of the changes in biodiversity predicted under global change? Knowledge of the role of biodiversity in ecosystem function is underdeveloped. More research is needed on how species composition feeds back to influence climate and land use.

Mitigation strategies. We have presented some of the types of management strategies that will be needed to cope with global change. Actual development and evaluation of alternative techniques for moving species, managing disturbance, controlling exotics, and other coping strategies merit considerable attention.

Conclusions

All ecological systems are dynamic and variations in climate, disturbance, and other ecological processes are required for maintaining some species and communities. However, change in biodiversity over the last century has been accelerated substantially by human land use and, possibly, by human-induced changes in climate. Rates of change in biodiversity are likely to be even greater in the near future. Our generation and the next one face the novel situation of having prior knowledge of the impending change. We also have increasingly sophisticated sets of data and tools for understanding and managing this change. How we use this knowledge and these resources may determine our well-being under global change. We draw the following conclusions from this review.

- Land use and, to a lesser extent, climate have changed substantially over the past century, causing important shifts in the abundance and distribution of species, communities, and biomes.
- Future changes in climate and land use are likely to be of a magnitude that cause even greater changes in biodiversity: The distributions of some species, communities, and biomes are likely to expand while others contract, and entirely new communities of species may form.
- The resulting changes in biodiversity are likely to feed back and influence land use, climate, and human well-being.

- There is considerable uncertainty in the magnitude and, in some cases, the direction of climate and land-use change expected in the future, as well as in the responses of ecosystems and organisms. The pace of land-use and climate change is likely to be rapid relative to the adaptability of species, leading to rapid shifts in species ranges, extinctions, and disequilibrum ecosystem dynamics. "Consequently, the only outcome that can be predicted with virtual certainty is major surprises. The only forecast that seems certain is that the more rapidly the climate changes the higher the probability of substantial disruption and surprise within natural systems" (Root and Schneider 1993, p. 267). Substantial investment in research and assessment will be needed to reduce uncertainties in the interactions between climate, land use, and biodiversity.

- Some level of uncertainty will remain, however, and policymakers and managers will benefit from incorporating consideration of this uncertainty in future outcomes—and the risk of those outcomes—into their decisionmaking.

- Current thinking on strategies and methods for coping with global change is underdeveloped. A comprehensive program of research, planning, and adaptive management would better allow society to understand, manage, and cope with global change before the changes erode biodiversity and human well-being.

- Because of the spatial scale of global change, coping strategies will require a new level of cooperation among public and private land stewards and among nations.

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