

Ecosystems

& Global **climate change:**

**A Review of Potential Impacts on
U.S. Terrestrial Ecosystems and Biodiversity**

Prepared for the Pew Center on Global Climate Change

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Foreword *Eileen Claussen, President, Pew Center on Global Climate Change*

Natural ecosystems are one of our most precious resources, critical for sustaining life on the planet. The benefits humans derive from ecosystems are varied, from marketable products such as pharmaceuticals, to recreational opportunities such as camping, to ecosystems services such as erosion control and water purification. For many people, nature plays a powerful spiritual and aesthetic role in their lives, and many place a high value on the existence of wilderness and nature for its own sake. Despite the critical roles ecosystems play, these areas are increasingly threatened by the impacts of a growing human population through habitat destruction and air and water pollution. Added to these stresses comes a new threat — global climate change resulting from increased greenhouse gas concentrations in the atmosphere.

“Ecosystems and Global Climate Change” is the fifth in a series of Pew Center reports examining the potential impacts of climate change on the U.S. environment. It details the very real possibility that warming over this century will jeopardize the integrity of many of the terrestrial ecosystems on which we depend. Among the many key issues raised are:

- *With warming, the distribution of terrestrial ecosystems will change as plants and animals follow the shifting climate.* The eastern United States will likely lose many of its deciduous forests as the climate zones shift northwards, while more mountainous regions, like portions of the West, will see species and ecosystems migrate up mountain slopes from lower elevations.
- *Both the amount and rate of warming predicted represent a threat to our nation's biodiversity.* Certain species may face dwindling numbers and even extinction if they are unable to migrate fast enough to keep up with the changing climate. Likewise, as warming shrinks the zone of cold conditions in upper latitudes and on mountains, the future of species that depend on such climates will be in jeopardy.
- *Climate change is likely to alter ecosystem composition and function — that is, which species make up an ecosystem and the way in which energy and materials flow through these systems.* These modifications are bound to alter the amount and quantity of the various goods and services ecosystems provide.
- *Ecosystems are inherently complex and difficult to model, and our ability to predict exactly how species and ecosystems will respond to a changing climate is limited.* This uncertainty limits our ability to mitigate, minimize, or ameliorate the effects of climate change on terrestrial ecosystems. In order to maximize nature's own potential to adapt to climate change, we must continue to support existing strategies to conserve biodiversity and protect natural ecosystems.

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Executive Summary

Climate is the single most important factor determining the geographic distributions of species and major vegetation types. It also influences the properties of ecosystems and the flows of energy and materials through them.

Global warming of the magnitude anticipated — a 1°C to 4°C (1.8°F to 7.2°F) increase in global mean temperatures over this century — will cause major changes in ecosystem distributions in the United States. In the eastern United States, these changes will result in a general northward shift in vegetation types. Results are more complex in the western United States due to local topography variation and small-scale climatic variations that result in complex, small-scale changes rather than broad northward shifts. The potential exists for significant reductions in the geographic extent of some ecosystems, especially those occurring in colder locales.

These shifts in major vegetation types due to global warming parallel the responses of the individual species that comprise these ecosystems. Thus, with global warming, shifts in the distributions of individual species are expected — in particular, a general poleward movement of distributions. Species have shifted their distributions in the past in response to changing climates; however, estimates of the rate of warming suggest that it may occur relatively quickly, some 10 times faster than the warming at the end of the recent glacial maximum, for example. It is not known whether species will be able to keep up with the rapidly shifting climatic zones. It is likely that some species will be unable to move at these high rates and hence may gradually die out as climatic conditions become increasingly unsuitable. The more rapid the rate of climate change, the greater the potential for this filtering effect. With higher temperatures, less of the earth will experience the cold conditions required by arctic and alpine species. As warming proceeds, these habitats are expected to decrease in size, leading to populations that are more isolated and to higher probabilities of extinction over time.

Climate change will also influence the functioning of ecosystems — the characteristic ways in which energy and chemicals flow through the plants, herbivores, carnivores, and soil organisms that comprise the living components of ecosystems. Models of overall changes in plant productivity indicate a wide range of possible changes across the lower 48 states, from slight declines (averaging 0.7 percent) to large increases (39 percent). Part of the uncertainty reflects poor understanding of how changes in temperature, moisture, and concentrations of carbon dioxide interact in influencing plant growth. Regional changes in productivity are not homogeneous, however, with some areas in the United States experiencing gains and others declines. For example, some scenarios show increases in plant productivity in the southeastern United States, whereas others showed large decreases under the influence of drier conditions. At the same time that increasing temperatures may lead to higher plant growth, they may also lead to higher decomposition rates and hence to increases in the rate at which carbon dioxide is being added to the atmosphere. It may be possible to increase the amount of carbon stored in ecosystems, and hence temporarily slow the rate of accumulation of carbon in the atmosphere (which comes primarily from the burning of fossil fuels) by planting forests on lands that currently do not support forests and by maintaining or increasing areas of mature and old growth forest.

+ Research on ongoing ecosystem change for several ecosystem types suggests that the effects of global warming on terrestrial ecosystems may already be altering ecosystems properties and species distributions. Nonetheless, there are substantial uncertainties as to how climate change will affect ecosystems and biodiversity in the United States. These uncertainties stem from not knowing the exact pattern of regional climate change as well as questions about how these patterns will affect the complex interactions and feedbacks among species and climatic conditions that characterize ecosystems. The effects of climate change on ecosystems and species are likely to be exacerbated in ecosystems that already are under pressure from human activities, including air and water pollution, habitat destruction and fragmentation, and the introduction of invasive species.

+ The effects of climate change on ecosystems threaten to jeopardize the numerous economically valuable goods and services that ecosystems provide to human societies, including services often undervalued in traditional economic analyses. In some cases, climate change will directly influence economic returns by affecting harvest levels; for example, warming-induced loss of salmon habitat from the United States would have a direct economic impact. Less easily measured are the potential effects of reduced

species diversity on the ability of ecosystems to maintain local environmental quality; for example, removing pollutants from air and water and controlling soil erosion. Ultimately, the value of ecosystems must also be considered in a broad context, including the moral, cultural, and aesthetic values of ecosystems and species.

Efforts to lessen the detrimental effects on species and ecosystems from climate change should focus on maintaining habitats as well as on maintaining overall ecosystem structure and species composition. Thus, adaptation to climate change may benefit from existing strategies to conserve biodiversity, such as reducing fragmentation and degradation of habitats, increasing connectivity among habitat blocks and fragments, and reducing external anthropogenic environmental stresses. However, the ability to actively manage ecosystems to ameliorate the effects of climate change by, for example, actively assisting plant species to migrate, is constrained by lack of understanding and by the complexity of the underlying ecological systems. Even the seemingly simple task of reintroducing plants into former parts of their range has met with little success so far.

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I. Introduction

The earth supports an enormous array of natural (i.e., largely unmanaged) ecosystems, inhabited by an overwhelming diversity of living organisms.

Critical for sustaining life on the planet, these ecosystems provide many goods and services that are of direct value to humans (see Box 1). Despite these benefits, however, most ecologists agree that human society is in the midst of an ecological crisis. An ever-increasing human population has affected and altered natural ecosystems in many ways through air and water pollution, species loss, habitat destruction, the introduction of invasive exotic species, and through other by-products of development and population growth.

Added to these existing pressures on ecosystems comes a new threat — the potential for rapid warming of the planet under the influence of increasing concentrations of greenhouse gases in the atmosphere, primarily from fossil fuel combustion and deforestation. Climate is a major factor controlling the distribution of species and the functioning of ecosystems (i.e., the characteristic way in which ecosystems modulate flows of energy and materials). As a result, there is widespread concern among scientists and decision-makers over the potential impacts of significant and rapid human-caused climate change on natural ecosystems. The potentially serious nature of climate change effects on species and ecosystems is reflected in the United Nations Framework Convention on Climate Change, which recognizes changes both in species composition and the functional roles of ecosystems as critical standards for setting emissions targets and limits to climate change (UNFCCC, 1992).

This paper provides an overview of some of the potential effects of global warming on natural terrestrial ecosystems and their component species in the United States.¹ Rather than providing a comprehensive review of the literature, which is beyond the scope of this series, this paper instead provides a review of key findings, concepts, and information gaps.

Box 1

Ecosystem Goods and Services

Aside from their intrinsic value, natural ecosystems also provide many goods and services of use to society (Costanza et al., 1997; Daily, 1997; Ehrlich and Ehrlich, 1992). These include:

- **Marketable products** — Humans derive a variety of direct economic benefits from harvesting or collecting products from natural ecosystems. Examples include timber, fish from fresh water or marine systems, and pharmaceuticals from a variety of ecosystems.
- **Recreation** — Natural ecosystems provide the settings for a wide variety of recreational opportunities including camping, boating, sports fishing, hunting, and hiking.
- **Maintenance of species** — There are a variety of reasons (discussed elsewhere in this report and in extensive literature) for preserving biodiversity. Natural ecosystems represent the major reservoir of biodiversity.
- **Aesthetic and spiritual experiences** — Many people derive enjoyment and comfort from experiencing nature or from simply knowing that minimally disturbed natural ecosystems exist and will be available for future generations to enjoy.
- **Ecosystem services** — Through their normal functioning, natural ecosystems provide many life-support services for the planet and help maintain local environmental quality. Examples include: nutrients in the soil, absorption of carbon dioxide and production of oxygen by plants, regional climate regulation, long-term sequestration of carbon, removal of pollutants from air and water, control of erosion, and control of pests and pathogens.

In virtually all cases, the quality and amount of goods and services derived from an ecosystem are related to the integrity and condition of the system. An ecosystem that is stressed or is being disrupted is unlikely to provide

the same quality or quantity of goods and services as a healthy or normally-functioning ecosystem. For example, boaters and fishers will normally not utilize polluted lakes or rivers, and a forested area that is cleared for another purpose no longer provides most of its original goods and services.

An area of active research and debate is the valuation of ecosystem services. Because many of the services are unrecognized, under-appreciated, or difficult to value, they are generally ignored when actions are taken that might impair or destroy the capacity of an ecosystem to provide services. One of the few examples of a reasonably successful effort to estimate the value of ecosystem services involves the decision by New York City to restore the watershed in the Catskill Mountains that provides drinking water, rather than constructing and maintaining an expensive water purification plant (Chichilnisky and Heal, 1998). The City chose to invest between \$1 billion and \$1.5 billion to purchase and restore land in and around the watershed as a means to reduce the levels of sewage, fertilizers, and pesticides that had caused the quality of drinking water to fall below U.S. Environmental Protection Agency standards. The use of natural ecosystems to filter the water was expected to save \$6 billion to \$8 billion over 10 years compared with the construction and operating costs of a filtration plant. Globally, terrestrial ecosystems are providing an important service that helps to subsidize global economic activity by absorbing and storing more than one quarter of the CO₂ emissions due to humans (see Box 3).

If climate change disrupts the structure or functioning of ecosystems, then a likely outcome is a diminished capacity of ecosystems to provide valuable services. It will be important for decision-makers to consider how climate change might affect the full range of goods and services provided by ecosystems and take this into account when decisions are made concerning climate policy.

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Ecosystems and global climate change

II. Background

A. The Role of Climate in Biological Systems

The pivotal role of climate in determining the geographic distributions and ecology of plants and animals has been recognized since at least the early 1800s and is readily observed in the current distribution of natural vegetation (Brown and Lomolino, 1998; Holdridge, 1947). For instance, major types of vegetation, such as rainforest, grassland, desert, deciduous forest, conifer forest, and tundra occur at similar latitudes and altitudes on different continents. This variation in vegetation observed as a function of distance from the equator and height above sea level parallels variation in temperature, documenting the strong role that temperature plays in determining the distribution and character of vegetation.

Superimposed on these temperature-determined changes in vegetation are changes due to variation in moisture. The important influence of moisture on vegetation is illustrated by the change observed in vegetation from coast-to-coast across the United States. On average, there is a decrease in precipitation with increasing distance from either coast, and this decrease is reflected in the character of the vegetation. The natural vegetation along most of the coastlines is forest (shrublands in Southern California), whereas grasslands and desert dominate most of the interior of the United States. Additional complexity is caused by mountain ranges such as the Sierra Nevada, Cascades, and Rocky Mountains. The windward sides of these mountain ranges receive greater amounts of precipitation and support relatively lush forests, whereas the leeward sides, which are in rain shadows, receive less precipitation and are characterized by sparser forests and semi-desert or desert vegetation. These patterns can be seen in a map of the potential distribution of natural vegetation types (that is, vegetation types as they presumably existed before European settlement) for the continental United States under present climate, included in Figure 1 on page 9.

In addition to its important role in controlling the distribution of vegetation, climate strongly influences the physical appearance of vegetation. The dominant plant species in a region tend to evolve

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common traits in response to the climate of a region, such as waxy leaves that prevent desiccation. The traits of the individual plant species determine the overall appearance of the vegetation of a climatic region. Thus, although the species generally differ from region to region, areas with similar climates often have vegetation of similar appearance. For example, the forests of high northern latitudes are dominated by needle-leaved conifers, whereas deserts worldwide are dominated by shrubs with small leaves and by spiny succulent plants of various types. Likewise, whereas the Mediterranean-type ecosystems found in five isolated regions of the world (the Mediterranean region, Southern California, Chile, South Africa, and western Australia) have virtually no species in common, they show convergence in their general appearance.

Other evidence for the important role of climate comes from paleoecology — the study of ecosystems of the distant past. In particular, there is abundant evidence that the expansion and contraction of the continental glaciers in the Northern Hemisphere during the Pleistocene resulted in southward and northward migrations of plant species (Brown and Lomolino, 1998). This kind of paleoecological data helps provide the basis for predictions that anthropogenic climate warming will result in significant poleward shifts in the distribution of individual plant species and vegetation types.

Climate is so important in determining the geographic distribution of plant species and vegetation types that relatively precise quantitative relationships between climatic variation and distribution patterns often can be derived. Ecologists have used the concept of a "climate envelope," which refers to the range of climatic conditions over which a species or vegetation type occurs, to provide a basis for relatively simplistic predictions about how future climate change might affect distributional patterns (Box, 1981; Emanuel et al., 1985). The approach simply assumes that the geographic range of a particular species or vegetation type is defined by the current climatic conditions over that range. If the climate warms and climatic zones shift poleward, one can predict a new geographic range within which the original climatic conditions still exist. To survive climate change, most plants must migrate into this new region.

While the climate envelope approach may be useful in providing a general indication of the responses of plants to climate change, it ignores other factors that might also influence the distributions of species and vegetation types. For instance, some plants are adapted to specific soil types, such as soils derived from serpentine rock or limestone, whose occurrence is unrelated to current climate. In addition, competition and other interactions among species can influence distributions. As a result,

organisms often occur in only a subset of their climatically suitable range, giving rise to the concept of fundamental vs. realized niches. The fundamental niche is the range of physical environmental conditions over which individuals of a species can survive and reproduce, whereas the realized niche refers to the actual range of conditions over which the species occurs. Competition and other species interactions may restrict a species to a realized niche that is much narrower than its fundamental niche. Ecologists interested in forecasting changes in the distributions of species or vegetation types must consider such complexities in their models (e.g., Prentice et al., 1992).

In general, climate is less important in determining the distributions and physical features of animals than it is for plants. Some large mammals (e.g., mountain lion) and birds (e.g., bald eagle) are able to tolerate a wide range of climatic conditions and are found over very broad geographic ranges, spanning many climatic zones and vegetation types. However, there are examples of animal species that are closely tied to specific climates, such as the dependence of polar bears on arctic sea ice to permit hunting for their prey in the winter. The distributions of many animals (such as many birds) are more dependent on features of the vegetation than of climate. As a result, the effects of climate on these animals may be largely indirect. Because climate has stronger and more direct influences on plants, the effects of a change in climate tend to be easier to document for these organisms, and far more studies of climate effects have been conducted for plants than for animals. For these reasons, this report focuses on impacts of climate change on plants.

In addition to influencing the distributions and appearances of organisms, climate also affects other ecosystem properties. Climate and vegetation interact to determine the characteristic soils in a region and different climatic zones are characterized by different soil types (except where the presence of unusual rocks such as serpentine result in unique soils). Climate also plays a central role in determining the characteristic disturbance regimes of an area, such as the frequencies of forest fires or hurricanes. Climate is very important in determining how quickly plants grow, and there is a good correlation between climatic conditions and Net Primary Productivity (NPP) — the total amount of plant growth per unit area per year. The amount of carbon stored in an ecosystem is also dependent on climate through effects on the stature of vegetation (trees vs. shrubs vs. grass) and on the amount of carbon stored below ground as peat or other soil organic matter.

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A caveat regarding the role of current and future climate in determining the distributions of vegetation types and plant and animal species concerns human activities. Humans have drastically altered the landscapes of much of the world. In many areas, conversion of natural vegetation to agriculture or other human uses has nearly eliminated the natural vegetation and many native species. In other cases, the effects are more subtle. The overall appearance of the landscape may not be that different, but alterations of fire and grazing regimes, introductions of invasive exotic species, and pollution have resulted in significant changes in the character and composition of natural ecosystems. Thus, rather than being superimposed on pristine native ecosystems, climate change is being superimposed on ecosystems already exposed to and altered by many other stresses (see Section III.E).

B. Global Climate Change

The average surface temperature of the earth has warmed by about 0.6°C (1°F) since the late 1800s, largely due to increased atmospheric greenhouse gas concentrations (Wigley, 1999). As these gases continue to accumulate, the earth's temperature is expected to continue to rise, with models predicting an increase of 1°C to 4°C (1.8°F to 7.2°F) over the next century (see Wigley, 1999). In general, models predict that the amount of warming will be noticeably greater in the United States than for the planet as a whole, although regional patterns within the United States are more difficult to predict (Wigley, 1999). Future regional-scale precipitation changes remain particularly difficult to predict, and changes in the frequency and severity of extreme weather events such as storms are uncertain (Wigley, 1999). Overall, these changes will appear as a general shift of climatic zones towards the poles as warmer temperatures reach further north in the United States.

From an ecological perspective, the magnitude of the expected warming is highly significant. For example, the surface of the planet was only approximately 5°C (9°F) colder on average during the recent Ice Age some 18,000 years ago. However, although the warming can be expected to have major ecological effects, the exact nature of these effects is difficult to predict with certainty. Part of the uncertainty rests with the state of climate modeling itself, especially uncertainties concerning regional temperature and precipitation effects. In addition, biological systems are remarkable for their complexity and as a result are very difficult to model and understand. Basic information required to understand likely biological responses to global warming, such as the maximum rates at which populations can move from place to place, how long they can persist in the face of unfavorable conditions, and the combined effects of higher temperatures and increased carbon dioxide (CO₂), are poorly understood.

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+ **Ecosystems** and global climate change

III. The Responses of Biological Systems to Global Warming

Based on all the available evidence from experiments, observations, and computer modeling, a change in climate of the magnitude predicted by climate models is expected to have significant effects on the distribution of vegetation types and species and on the functioning of ecosystems. For the purpose of this report, three major types of ecosystem changes are distinguished: (1) changes in the geographic distribution of vegetation types, (2) changes in ecosystem processes such as productivity, and (3) changes in the distributions and abundances of individual species. However, it is important to recognize that many if not most ecosystems will experience all three types of effects simultaneously and that these effects are interrelated. Thus, a change in vegetation type is likely to occur simultaneously with changes in species distributions, and the two together will modify important ecosystem processes. Equally importantly, these changes will occur within a milieu of existing anthropogenic pressures, especially habitat loss and fragmentation.

A. Impacts of Global Warming on the Geographic Distributions of Vegetation Types

Climate change over the next century or so will likely ultimately result in changes in the distribution of major vegetation types, just as past climate changes have affected vegetation distribution.

Early analyses of how climate change might affect vegetation patterns utilized variations of the climate envelope approach (e.g., Emanuel et al., 1985). Relatively simple models based on the correlation between climate and vegetation distribution were used to project how vegetation zones might shift with climate change. Over the past 15 years, increasingly sophisticated computer models have been developed that incorporate more fundamental ecological mechanisms (e.g., physiology, competition, nutrient cycling) and replace the simpler correlational approaches of climate envelopes. While there is little doubt that today's models represent improvements over earlier ones, they still suffer many limitations, and the models cannot predict with accuracy what will happen as climate changes. Therefore, the results from these models should be taken as indicative, but not as conclusive. It is important to note, however,

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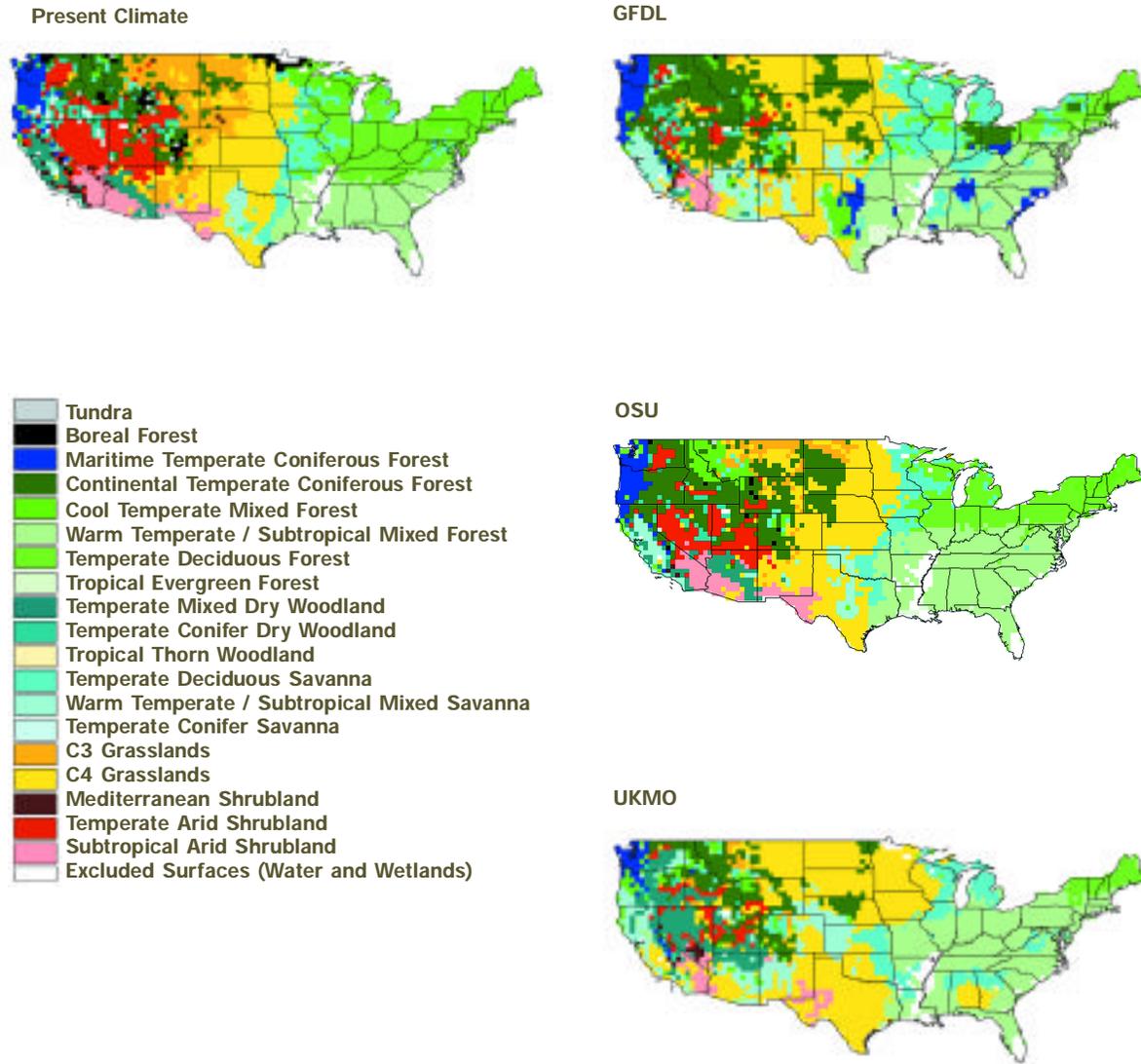
that the existence of uncertainty does not imply that the “no-change” option is likely. In fact, more extreme change than predicted is often as likely as less extreme change.

In discussions of vegetation models, it is important to distinguish between shorter-term transient responses to climate change and longer-term equilibrium responses. Until a few years ago, the only models available for projecting regional or global changes in vegetation distribution were equilibrium models. An equilibrium analysis assumes that the current vegetation distribution more or less reflects the conditions associated with the current climate. The eventual effects of climate change are simulated by running the vegetation model with a future climate scenario, usually based on the results of a general circulation model (GCM). The future climate scenarios used in most analyses have been of an atmosphere stabilized at twice the pre-industrial CO₂ concentration. The analysis then projects the future equilibrium distribution of vegetation under the new stable climate. The analysis does not involve projections of how fast the changes will occur, how long it will take to reach a new equilibrium, what the vegetation might look like during the transition period, or what might happen beyond a doubling of CO₂ concentrations.

Figure 1 presents results from equilibrium analyses that were conducted as part of the Vegetation-Ecosystem Modeling and Analysis Project (VEMAP) (VEMAP Members, 1995), a large collaborative effort to evaluate potential effects of climate change on vegetation distribution and ecosystem processes in the lower 48 states. In the figure, projections of vegetation distribution using one of the three vegetation models used in VEMAP (i.e., MAPSS) are displayed under current climate conditions and under doubled CO₂ climate scenarios as generated by three GCMs. (These maps are of potential vegetation distribution, not actual distribution, because, aside from increased CO₂ concentrations, the models do not include anthropogenic impacts.) The three GCMs provided a range of climate change scenarios, with the average temperature increase for the United States varying between 3.0°C and 6.7°C (5.4°F and 12°F)² and precipitation increase between 4 and 21 percent. It is currently not known which of the vegetation and GCM models is better or more accurate: the various models represent the best attempts of different groups of scientists. The differences in results among models reflect scientific uncertainty about how climate will change and how vegetation will respond. All the models predict significant change, but they differ in the details. In general, the climate and vegetation models tend to agree more on broad regional patterns than on details at the local scale.

Figure 1

Effect of Doubled CO₂ Concentrations on **Vegetation Distribution** in the Lower 48 States



The effect of climate change and doubled atmospheric CO₂ concentration on vegetation distribution in the lower 48 states. Results are shown for one vegetation model (MAPSS) run under four climate scenarios (present climate and three scenarios of doubled atmospheric CO₂ concentrations: GFDL, OSU, and UKMO). Notice the general shift of vegetation types to the north, especially in the eastern part of the country. Patterns of change in the West are more complex because of greater topographic variation. In the complete set of VEMAP simulations, three vegetation models were used, as summarized in Table 1.

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The VEMAP results illustrate that the distribution of natural vegetation types could be substantially altered by climate change resulting from a doubling of the concentration of CO₂ in the atmosphere. The potential effects are most easily observed in the eastern United States where climatic gradients are simpler because there are fewer mountains. Here, a general northward shift of vegetation types occurs. Some vegetation types such as boreal forest and certain kinds of deciduous forest (including cool temperate mixed forest and temperate deciduous forest) either are eliminated or are substantially reduced in area. The warm temperate mixed/evergreen forest type of the southeastern United States expands at the expense of these other forest types. However, in some of the scenarios, parts of the Southeast become drier and grasslands or savannahs replace the current forest. If correct, this latter scenario would have important implications for agriculture and forestry in the Southeast. This is an example of how the implications of ecological effects of climate change will vary geographically: some areas may be adversely affected while other areas may experience less change, or experience changes that might be considered desirable.

General conclusions about vegetation change in the western United States are more difficult because of the topographic complexity of the West (i.e., mountain ranges resulting in steep temperature and precipitation gradients), which is not adequately represented in this relatively coarse resolution analysis. However, most scenarios show that the changes in vegetation types occur as complex, smaller-scale changes rather than as broad northward shifts. In some scenarios, there is a replacement of desert vegetation by grassland or shrubland.

Table 1 shows the percentage of the continental United States covered by each of seven major vegetation types (condensed from the 21 types used in the VEMAP analysis by combining similar types) for each of the climate and vegetation model combinations. Substantial changes in the area covered by several of the vegetation types are indicated. For instance, conifer forests potentially would cover about 11 percent of the area of the United States at present (if humans had not altered the landscape), whereas under a doubled CO₂ climate, they would cover as little as 6.5 percent or as much as 22.1 percent of the area of the United States. Similarly, subtropical shrublands currently would cover 4 to 5.4 percent of the area, and with climate change would cover anywhere between 1.8 and 14.6 percent of the area. It is important to remember that these numbers reflect the area covered by the vegetation types and hence provide only a partial picture of vegetation change. The area of a certain vegetation type might remain nearly constant, but its geographic distribution might shift substantially. All of the models

Table 1

Percent of Lower 48 States Covered by Major Vegetation Types under Doubled CO₂ Scenarios

Vegetation Model	Climate Scenario	Vegetation Type ¹						
		Tundra	Conifer Forest	Broadleaf Forest	Savanna/Woodland	Temperate Shrubland	Grassland	Subtropical Shrubland
MAPSS	Contemporary	0.2	10.9	32.6	14.8	10.2	27.3	4.0
	GFDL	0.0	22.1	30.2	21.1	2.3	22.5	1.8
	OSU	0.0	17.1	36.3	13.5	6.2	22.7	4.1
	UKMO	0.0	9.4	28.6	23.7	3.0	32.9	2.4
BIOME2	Contemporary	1.0	11.4	34.6	15.1	13.0	19.4	5.4
	GFDL	0.1	10.6	40.0	19.2	8.0	18.4	3.7
	OSU	0.1	8.8	30.8	17.9	12.8	21.4	8.1
	UKMO	0.0	6.6	33.1	17.2	7.0	26.9	9.4
DOLY	Contemporary	0.4	10.7	31.0	24.5	11.5	16.7	5.1
	GFDL	0.9	7.8	38.3	28.1	2.9	15.3	6.7
	OSU	0.5	7.6	31.1	24.4	1.5	24.7	10.1
	UKMO	0.7	6.5	36.0	28.9	1.7	11.6	14.6

Percent of the lower 48 states covered by major vegetation types under scenarios of doubled CO₂ concentrations and accompanying climate change. Three vegetation models (MAPSS, BIOME2, and DOLY) were used to simulate the vegetation types and each was run for four climate scenarios (contemporary climate and three doubled-CO₂ scenarios [GFDL, OSU, and UKMO]). Simulations were undertaken by the VEMAP project (VEMAP Members, 1995). Because of the variability among simulations, few overall generalizations are possible, except perhaps for a reduction in the area of temperate shrublands.

¹Vegetation types are aggregates of the 21 original types used in the VEMAP project and in Figure 1.

predict substantial changes in the locations of vegetation types across the United States, with 44 to 73 percent of the land area experiencing a change in vegetation type (Table 2). These results are similar to those from other analyses, as reported by Neilson (1993).

One important limitation of virtually all vegetation models used to date in these sorts of regional assessments is that they only treat natural (i.e., unmanaged) vegetation and fail to incorporate the impacts of humans on the environment from activities such as logging, agriculture, and other activities that alter land cover. Similarly, they do not include the effects of air pollution such as the deleterious effects of ozone on vegetation. As a result, these models predict potential natural vegetation and not actual land cover as modified by humans. In some cases, these human-induced changes in land cover will have an important influence on the responses of vegetation

Table 2

Percent of Land Area of Lower 48 States Exhibiting Vegetation Type Change under Doubled CO₂ Scenarios

Climate Scenario	Vegetation Model		
	MAPSS	BIOME2	DOLY
GFDL	64	61	68
OSU	44	49	58
UKMO	70	70	73

Percent of the land area of the lower 48 states that exhibited changes of vegetation types under scenarios of global warming. Three vegetation models (MAPSS, BIOME2, and DOLY) were used to simulate 21 vegetation types and each was run for four climate scenarios (contemporary climate and three doubled-CO₂ scenarios [GFDL, OSU, and UKMO]). Simulations were undertaken by the VEMAP project (VEMAP Members, 1995). Although the models predict different patterns of change (see Table 1), they all agree in that considerable change is predicted.



distributions to climate change. Clearly, areas already mostly cleared for agriculture or cities will not revert to natural vegetation. It also is possible that these human-dominated ecosystems will serve as barriers and prevent or slow the migration of some species to new regions. In parts of the country where vegetation cover is more natural, the projections of the models may be more realistic. Another limitation of the models is that they generally do not include the effects of natural fires, herbivores, or disease. It is unclear how climate change will alter the occurrence of these phenomena, but in some cases, the effects could be major and result in vegetation patterns not predicted by the models. Finally, the models do not simulate important soil properties that may be important in determining whether individuals of a species can establish and grow in a new region. Thus, at least in some cases, it is not clear whether suitable soils will exist for species that have to migrate to new regions.

In the past 5 years, considerable progress has been made in addressing some of the weaknesses and limitations of the equilibrium models used in VEMAP. In particular, in place of equilibrium analyses, most vegetation modeling groups have been working on dynamic models that simulate vegetation change over time. For example, Dynamic Global Vegetation Models (DGVMs) (Foley et al., 1996; Friend et al., 1997) simulate vegetation over the entire earth and can both reproduce vegetation change over the recent past and simulate future vegetation change in response to transient climate change. These models also explicitly integrate models of vegetation dynamics and of biogeochemical nutrient cycles, which were treated separately in VEMAP. In the past year, scientists have begun conducting simulations of future vegetation types using these new models; however, published results are not yet available.

B. Impacts of Climate Change on Ecosystem Processes

In addition to causing changes in the distribution of major vegetation types, climate change is also expected to affect the functioning of natural ecosystems, that is, the characteristic ways in which energy and chemicals flow through the plants (primary producers), herbivores (plant eaters), carnivores (meat eaters), and soil organisms that comprise the living components of an ecosystem. Measurement of the rates and pathways by which energy and materials enter, flow through, and are lost from ecosystems is one of the major approaches ecologists use to analyze ecosystems. Changes in these rates and pathways represent fundamental changes in the functioning of ecosystems. An additional major reason for interest in effects of climate change on ecosystem processes is that climate-induced changes in natural ecosystems may in turn lead to further feedback effects on the climate system. Some initial level of climate change may set in motion a series of effects and feedbacks that cause additional regional or global climate change. For example, increased decomposition of peatlands under global warming could lead to further increases of CO₂ in the atmosphere and to further warming.

Perhaps the most widely used and important measure of ecosystem functioning in terrestrial and aquatic ecosystems is Net Primary Productivity (NPP). NPP is a measure of the total amount of plant growth (i.e., considering all plants or at least all the dominant plants) per year in an ecosystem and is usually measured as grams of carbon in new plant material produced per unit of area per year (see Box 2). Since all other organisms ultimately depend on primary production by plants for their energy, a change in NPP represents a fundamental change in the functioning of an ecosystem. Changes in NPP also are likely to signal changes in potential human uses of ecosystems. For instance, the NPP of a forest is directly related to its capacity to produce timber, while the NPP of a grassland determines how much forage will be available for livestock or other grazing animals. The rate and total amount of growth by plants is affected not only by various environmental factors such as temperature and moisture supply, but also by the concentration of CO₂ in the atmosphere. In general, NPP increases as CO₂, temperature, or moisture supply increase, although at very high temperatures or under water-saturated conditions, the effect may be reversed.

Box 2

Plant Productivity vs. Ecosystem Carbon Storage (Understanding NPP, NEP, and NBP)

The distinction between plant growth (i.e., NPP) and net carbon storage in terrestrial ecosystems is potentially confusing. Ecologists have developed two additional terms, Net Ecosystem Productivity (NEP) and Net Biome Productivity (NBP), to help clarify the underlying concepts and to focus attention on the ecosystem processes that determine whether an ecosystem is accumulating or releasing carbon.

NPP is a measure of the total amount of plant growth per year in an ecosystem. It is measured as the difference between total carbon uptake through photosynthesis minus carbon lost back to the atmosphere through plant respiration (which provides energy for maintenance and new growth). NPP is such a fundamental process that any change in the NPP of an ecosystem indicates a change in the health of the ecosystem. An increase in NPP is not always desirable because the change itself can compromise ecosystem health. NPP normally will increase as the resources that limit plant growth (such as CO₂, nitrogen, or water) increase; this is a fairly straightforward response. If climate changes in an area, NPP may rise and then stabilize at a new level, or it may go down and then stabilize. Over the long term, NPP has to be positive (there has to be plant growth each year) or else there will be no life. Thus, NPP will be greater than zero unless an ecosystem is under severe stress or is somehow declining. However, just because NPP is positive does not mean an ecosystem is accumulating carbon from year to year.

Net Ecosystem Productivity (NEP) is a measure of the net exchange of carbon between the atmosphere and an ecosystem. It includes NPP but also includes the release of carbon through the process of decomposition, or the decay of dead organic matter by soil organisms (i.e., $NEP = NPP - \text{decomposition}$). In a mature or "climax" ecosystem, NEP may be zero or close to zero: carbon uptake through plant growth is balanced by carbon release through decomposition. The existing stocks of carbon are maintained, but there is no increase. A young forest will have a positive NEP and will be removing carbon from the atmosphere. As the forest matures, NEP will decrease and the forest will remove less carbon from the atmosphere.

The response of NEP to climate change or other environmental stress is more complex and difficult to predict than the response of NPP, because more processes are involved. NPP may go up as temperature increases,

but so may the rate of decomposition; thus, there may be no change or even a decrease in NEP. Possible interactions of changes in temperature with changes in water or nutrient availability add an additional layer of complexity. NEP typically is reported for time periods of a year or less and is somewhat of an abstract concept because it does not include additional ecosystem processes that help to determine the net carbon balance over long time periods.

NEP is not an appropriate measure of long-term carbon exchange, especially over large areas, because it neglects disturbance processes such as fire, forest clearing, insect infestation, or extreme weather events. These can all cause the release of large amounts of carbon into the atmosphere. To consider these, ecologists developed the term Net Biome Productivity (NBP), which is NEP minus losses of carbon due to disturbances (i.e., $NBP = NEP - \text{disturbance}$). It is measured (or estimated) for large regions and over long time periods, such as for the entire United States over a decade or century. NBP for a region should be zero over the long term if the ecosystem is in a stable state and carbon releases from disturbance are balanced by carbon uptake in growing stands. If climate changes, it could cause NBP for a region to be negative or positive over a relatively long period as the entire system adjusts to the new climate. For instance, following the last retreat of continental glaciers, NBP was positive for thousands of years (and might still be in some regions) as vegetation established itself and organic material gradually accumulated in soils. NBP also can remain positive over extremely long periods if organic matter can be protected from decomposition, fire, and other disturbances. Peat formation in cold wet areas is an example.

The distinctions between NPP, NEP, and NBP are critical to an understanding of the role of terrestrial ecosystems in the global carbon cycle and as a net sink for carbon. In particular, it is important to recognize that NPP can be positive while NEP is stable or negative. Similarly, NEP can be positive for a plant stand, while NBP is stable or negative for a larger region. Finally, even NBP is unlikely to remain positive indefinitely for the entire earth, especially considering the many ways in which human activities disturb natural ecosystems and cause reductions in the amount of carbon stored.

Although changes in climate will affect NPP, precise predictions for large regions such as the United States are difficult to make. These difficulties arise because of the variety of factors besides temperature, precipitation, and CO₂ that influence plant growth, including the supply of nitrogen and other nutrients, soil properties, and vegetation type.

The potential effects of climate change on NPP in the United States were evaluated as part of the VEMAP model intercomparison. For this analysis, three models of ecosystem processes (i.e., biogeochemistry models) were used in combination with the three GCMs and the three vegetation models that

were used in the analysis of vegetation distribution. The results for the United States as a whole ranged from a decrease in NPP of 0.7 percent to an increase in NPP of 39.7 percent (Table 3).

Figure 2 shows regional patterns of change for a selection of model combinations. NPP changes in a

particular region depend on the changes in both temperature and precipitation. In many areas, especially in the Southeast or Southwest, NPP will increase only if there are increases in precipitation sufficient to offset the increased evaporation caused by higher temperatures.

The values for NPP for the United States as a whole and for any particular location vary widely depending on the combination of models used, indicating that current understanding is insufficient to make precise projections. Despite this variation, these results indicate that the magnitude of the potential climate change over the next century is likely to substantially alter NPP values for natural ecosystems in the United States. These changes will not be homogeneous however, with some regions experiencing higher NPP, and others lower NPP. In general, one can view an increase in NPP as a positive impact, because it means that timber or forage production will increase. However, it may also result in changes in species composition or other ecosystem attributes that are considered undesirable. On the other hand, a decrease in NPP would almost always be viewed as a negative impact.

Table 3

Percent Change in Net Primary Productivity (NPP)

for the Lower 48 States for Climate Change Scenarios

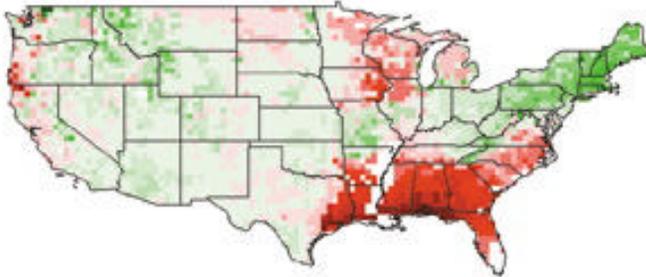
Vegetation Model	Climate Scenario	BGC	CENTURY	TEM
MAPSS	GFDL	20.4	29.2	37.2
	OSU	11.9	15.6	39.7
	UKMO	-0.7	20.3	32.4
BIOME2	GFDL	21.7	18.4	38.5
	OSU	7.4	11.3	27.0
	UKMO	0.4	12.2	27.8
DOLY	GFDL	20.1	20.4	39.0
	OSU	5.6	26.0	33.1
	UKMO	-0.1	14.7	33.2

Percent change of Net Primary Productivity (NPP) for the lower 48 states for climate change scenarios relative to contemporary climate. Three biogeochemistry models (BGC, CENTURY, and TEM) were linked with three vegetation models (MAPSS, BIOME2, and DOLY) and run under three doubled-CO₂ scenarios (GFDL, OSU, and UKMO). The simulated NPP values were subsequently compared with NPP values simulated under contemporary climate (VEMAP Members, 1995). Climate change scenarios generally resulted in an overall increase in NPP.

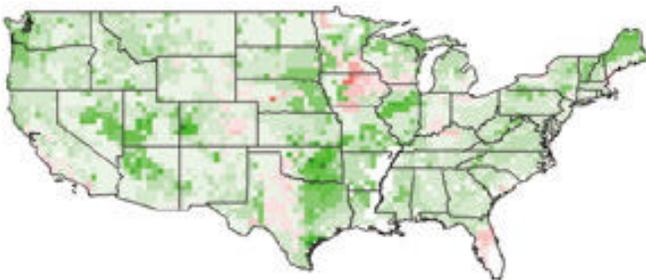
Figure 2

Simulated **Changes in Annual Net Primary Productivity (NPP)**
for Three Combinations of Models

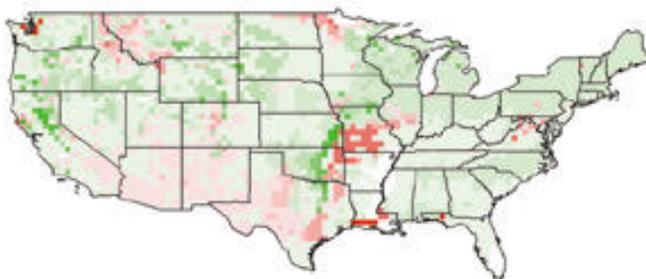
UKMO - MAPSS - BGC



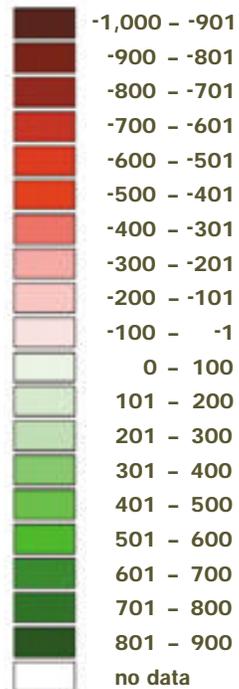
GFDL - BIOME2 - TEM



OSU - MAPSS - CENTURY



NPP (gC/m²/yr)



The three maps show the geographic distribution of changes in annual Net Primary Productivity (NPP) for three of the 27 results summarized in Table 3. Each map shows the results for a particular climate scenario linked to one of three vegetation models and one of the three biogeochemistry models. The color scheme represents changes from contemporary NPP (in units of grams of carbon per m² per year). In the complete set of VEMAP simulations, three biogeochemistry models and three biogeography models were used, hence 27 maps similar to the ones shown were generated.

Another approach for determining how climatic and atmospheric change may affect natural ecosystems comes from field experiments.³ Over the last two decades, scientists have conducted a large number of field experiments to evaluate how increases in atmospheric CO₂ concentrations, independently of associated global warming, may affect NPP and other ecosystem properties (Mooney et al., 1999). These experiments have involved either enclosing small plots in a chamber within which the level of CO₂ can be increased, or by surrounding larger plots (even with large trees) with arrays of pipes from which CO₂ is released. An example of the latter is the Free Air Carbon Dioxide Enrichment (FACE) experiment at Duke University, in which 30-meter diameter plots of loblolly pine forest are being exposed to elevated CO₂ concentrations (DeLucia et al., 1999). In both types of experiments, sophisticated sensors and computer controllers monitor the CO₂ level and atmospheric conditions to maintain CO₂ at the desired level. These studies have fairly consistently shown that NPP increases by approximately 15 to 20 percent when the CO₂ level is twice the pre-industrial level (Mooney et al., 1999). This increase is significant, but is far less than the level of growth stimulation observed in early experiments using single plants in pots in greenhouses. It is not clear whether such increases will be sustained indefinitely and whether they will ultimately contribute to a long-term increase in the amount of carbon stored in the ecosystems (that is, to the removal of CO₂ from the atmosphere and storage in living plants or soil organic matter — see Box 3). Various mechanisms that could cause the rise in NPP or carbon storage to gradually dampen are being investigated in ongoing experiments.

A number of “ecosystem warming” experiments also have been initiated to determine the effects of increased temperatures on ecosystem processes and species composition (Hart and Shaw, 1995; Arft et al., 1999; Shaver et al., in press). Because temperature can affect ecosystems in many different ways, and because of multiple pathways for feedbacks and interactions, evaluating or predicting the effects of temperature increases is not simple. Not surprisingly, the results to date are mixed (Shaver et al., in press). As with elevated CO₂ experiments, one objective of the warming experiments is to determine how increases in temperature will affect carbon storage. Photosynthesis and NPP may increase in certain ecosystems, but decomposition of dead organic matter also will increase. Since the response of photosynthesis and NPP is expected to plateau and even decrease as temperatures rise, while the rate of decomposition generally should continue to increase, climate change could result in a net release of carbon to the atmosphere from terrestrial ecosystems (and hence to a potential augmentation of global warming).

Box 3

Carbon Sequestration

An important service provided by terrestrial ecosystems is the storage of carbon (C) that otherwise might add to the amount of CO₂ in the atmosphere and thus contribute to further climate change.⁴ Terrestrial ecosystems are an important component of the global carbon cycle, and changes in these ecosystems could modify the global cycle of carbon. It is estimated that at least 2,200 Gigatons (1 Gt = 1 billion metric ton) of carbon are stored (sequestered) in terrestrial ecosystems, with about 600 Gt in living plant tissue (mainly forest trees) and at least 1,600 Gt in soil as soil organic matter (e.g., litter on the soil surface, humus in soil, and peat deposits) (IPCC, 2000). These amounts compare with the 775 Gt of C in the atmosphere and the annual addition of approximately 7.9 Gt to the atmosphere from human activities, primarily the burning of fossil fuels (Schlamadinger and Marland, 2000; IPCC 1996b). Terrestrial ecosystems currently absorb approximately 2.3 Gt of C per year, or over one quarter of the human emissions. At the same time, approximately 1.6 Gt of C are re-released from ecosystems to the atmosphere primarily as a result of deforestation.

The processes of photosynthesis, respiration, and decomposition are the links between carbon in the atmosphere and carbon in terrestrial ecosystems. Plants remove CO₂ from the atmosphere through the process of photosynthesis, which results in the production of living plant tissue. CO₂ is returned to the atmosphere through the processes of plant respiration and decomposition of dead organic matter in the soil. Animal (and human) respiration, which also returns carbon to the atmosphere, is insignificant compared with plant respiration and decomposition. Any change in the global balance between photosynthesis and respiration/decomposition will alter the amount of carbon that is sequestered in terrestrial ecosystems. Since the magnitude of these processes on an annual basis is very large, small changes could have dramatic implications for the balance and thus the amount of CO₂ entering the atmosphere.

Human activities can alter the global balance of photosynthesis and respiration/decomposition and thus alter the amount of carbon sequestered in terrestrial ecosystems. Since the origin of agriculture, the main effect of humans has been to promote the release of carbon from terrestrial ecosystems and thus increase the concentration of CO₂ in the atmosphere. Clearing of forests for agriculture or development results in the loss of most of the carbon stored in the trees; tilling of soil for agriculture results in

loss of carbon from soils. If human activities increase the incidence of fires in natural ecosystems, this also normally will result in a transfer of carbon to the atmosphere.

It also is possible for human activities to alter the balance in the other direction and thus promote sequestration of carbon. As a result of current societal concern about climate change, a great deal of research and discussion has focused on using ecosystems to retain or accumulate carbon, and hence partly offset CO₂ emissions and the buildup of CO₂ in the atmosphere. While the potential for increased storage appears to be small compared to the rate at which CO₂ is being emitted (Nilsson and Schopfhauser, 1995; Turner et al., 1995), terrestrial ecosystems might be used to help temporarily reduce the rate of atmospheric CO₂ accumulation. Ways to involve ecosystems in efforts to reduce the rate of buildup of atmospheric CO₂ include afforestation — the establishment of forests where they currently do not exist — preservation of existing forest, and use of biomass to substitute for fossil fuels and other more energy-intensive products (Schlamadinger and Marland, 2000). It is important to recognize that there will be net carbon storage while a forest is growing, but once the forest is mature (generally on the order of several decades to a century or more depending on the location and species), uptake of carbon by photosynthesis will be balanced by losses through respiration and decomposition. In order for a forest to continue to sequester carbon, it is necessary to harvest trees and use a high proportion of the biomass in long-lived products while also minimizing disturbance to the soil and the production of slash, both of which would result in the release of CO₂ to the atmosphere.

In addition to planting new forests, it also is possible to promote the sequestration of carbon through altered forest management practices. For example, in situations where logging is gradually reducing the average age of the forest, and hence the amount of carbon stored, it is possible to change harvesting practices to maintain the carbon stocks of old-growth and mature forests. Whether greater carbon benefits can be achieved by protecting existing forests or using forests for production of fuels or other products depends on site-specific factors (Schlamadinger and Marland, 2000).

Carbon also can be sequestered in soils through improved or altered management practices, such as restoration of degraded soils and various conservation tillage practices including no-till agriculture. These practices

Box 3 continued

will be most effective on soils that previously have lost soil carbon because of conventional agriculture or other activities that have depleted soils of organic matter that would otherwise be there in the absence of the disturbance.

Some of the potential implications of management of ecosystems to promote carbon storage are positive for biodiversity, such as increased forest cover, protection of old-growth forests, recovery of degraded forests, and increased rotation lengths in managed forests (Solberg, 1997). Other potential implications are negative, such as a return to forest management strategies based on a single product (in this case carbon). For example, management could lead to forests dominated by tree species that most efficiently sequester carbon. Many of the gains that have made modern forestry more ecologically sustainable have come from shifting away from management systems based on a single dominant product (timber) to those that consider the multiple benefits that forests provide, such as wildlife and aesthetic values. Efforts to use ecosystems to store carbon may be counterproductive if they encourage

plantation forestry or provide incentives to destroy primary forests. The habitat loss that occurs when more profitable uses for land are found is a primary contributor to species endangerment (Sagoff, 1996).

Preservation of existing old-growth forests, use of biomass to replace fossil-fuels, use of long-lived products, afforestation, conservation tillage, and similar land management practices represent important options for sequestering carbon from the atmosphere and thus slowing the buildup of CO₂ in the atmosphere. However, these practices cannot sequester all the CO₂ emitted by current human activities and so can only be one component of a combination of strategies.

While this discussion has focused on the future potential for increased carbon storage through land management strategies, terrestrial ecosystems currently are absorbing and storing approximately one quarter of human emissions. Thus, they already are providing an important service in decreasing the rate of CO₂ accumulation in the atmosphere.

The possibility also exists for indirect effects of warming on NPP and carbon storage. For instance, a recent modeling study predicted that warming could cause a decrease in soil moisture, which in turn could reduce the growth of white spruce in boreal regions of Alaska (Bonan et al., 1990). Recent observations support this conclusion (Barber et al., 2000). Experiments have not been underway long enough to determine how the changes in photosynthetic uptake of carbon will balance out against loss of carbon through decomposition in different types of ecosystems.

It has been common in experiments and modeling exercises to investigate the effects of a doubling of pre-industrial CO₂ atmospheric concentrations. However, atmospheric levels of CO₂ could continue to rise beyond a doubling of pre-industrial levels. Unfortunately, no experimental or modeling studies comparable in scope or sophistication to the ones discussed above have been undertaken to evaluate ecosystem responses to higher CO₂ levels or to more extreme climate change. There is no question that more extreme changes in climate will cause more extreme changes in ecosystems, including changes in the distributions of vegetation and species and changes in the functioning of the ecosystems.

Warming and elevated CO₂ experiments have been very important in improving understanding of how ecosystems may respond to specific changes in the environment and are critical to the development

of more realistic computer models. However, most experiments to date are single or, at best, two factor experiments (i.e., only CO₂ concentration or only soil temperature was varied). One has to be careful in extrapolating results from such simple experiments to the real world, where a variety of other factors are simultaneously operating, such as altered precipitation, nitrogen deposition, ozone, and land management.

While experiments and computer modeling are crucial tools for improving predictions about how ecosystem properties might change under an altered climate, evidence from actual measurements of current ecosystems shows that climate change is already affecting key ecosystem properties. As temperatures in northern high latitudes have increased over the past 100 years, scientists have begun to detect effects on ecosystems. For instance, satellite measurements of the greenness of the vegetation indicated that during the decade between 1981 and 1991, there was an increase in potential photosynthesis by approximately 10 percent and the length of the growing season increased by approximately 12 days (Myneni et al., 1997). Ground-based monitoring efforts in Europe also documented an increase in the growing season of about 11 days over a 34-year period (Menzel and Fabian, 1999). The observation of reduced growth of white spruce in Alaska mentioned above indicates the potential for negative impacts on ecosystem productivity in some regions. The gradual increase in atmospheric CO₂ during this time may also be contributing to some of the changes observed.

+ This discussion of the effects of climate change on ecosystem processes has focused heavily on NPP and aspects of carbon cycling (see Box 2) in part because of the potential for feedbacks to the climate system, especially through the potential of ecosystems to absorb or further increase the amount of CO₂ in the atmosphere. However, it is important to recognize that there are other important links between ecosystems and climate. Vegetation is a key factor in determining the exchange of energy and moisture between the earth's surface and the atmosphere, and the type of vegetation is particularly important in determining the rates of exchange. Thus, replacing dark colored evergreen trees with lighter colored surfaces (such as snow, grassland, or agricultural land) can have a large effect on local to regional climate through effects on evapotranspiration, windflow, and reflectivity of the surface. For instance, computer modeling studies have indicated that if climate warming causes conifer forests to replace tundra, regional temperatures could increase further because the dark forests absorb more energy than the more reflective, often snow-covered tundra (Bonan et al., 1992). This and other studies (e.g., Foley et al., 1994; Shukla et al., 1990; Levis et al., 1999) emphasize the multiple roles of ecosystems in modifying local and global climate.

C. Effects on Species and Communities

The important functions carried out by the earth's ecosystems are performed by the myriad species that make up ecosystems. For this reason, the responses of ecosystems to climate change can be predicted only in part by understanding the behavior of their convergent properties. One must consider the unique characteristics and responses of the individual species as well.

As a result of climate change, existing climatic conditions in many areas will become unsuitable for the species that currently live there, requiring them to migrate to survive. For example, predictions under doubled CO₂ concentrations of the distributions of 80 tree species that occur in the northeastern United States showed that nearly half of the species (36) shifted at least 100 kilometers (km) to the north, with seven shifting over 250 km to the north (Iverson and Prasad, 1998). The fact that species will have to move in itself is not alarming — most have done so in the past and, even in the absence of human interference in the global climate system, will undoubtedly do so again. However, several aspects of anthropogenic global warming are of particular concern, including the potential rapidity of the change and the possibility that certain alpine or polar ecosystems, which are typical of very cold conditions, could be greatly reduced in size or lost entirely. An additional concern — that the effects of climate change may be exacerbated under other human activities — will be considered in Section III.E. +

Global warming may require organisms to migrate at much higher rates than they have in the recorded past. During the retreat of the ice sheet after the previous Ice Age, trees on average moved at about 1 km per decade to keep up with the shifting climatic conditions (Huntley and Birks, 1983). Typical predictions of global warming imply rates of warming that are faster by roughly a factor of ten, requiring migration rates of some 10 km per decade (Davis, 1989; Dyer, 1995). Unfortunately, the migrational capabilities of species are poorly understood. Even for trees, which are particularly well-studied because of their commercial and aesthetic value and because of their great importance in creating habitat + for other species, it is uncertain whether past migrations represented maximum intrinsic capabilities (Davis, 1986; Huntley, 1989; Davis, 1989) or whether they can in fact move faster (Clark, 1998). For some organisms, such as highly mobile plant species and many animals, these potentially high future migration rates are unlikely to pose a problem. Weeds, for example, can migrate very quickly by virtue of their copious production of mobile seeds, ability to colonize a wide variety of habitats, and fast maturity.

Indeed, migration rates much higher than 10 km per decade were observed when cheatgrass invaded the western United States between 1880 and 1920 and when goldenrod invaded Europe between 1850 and 1875.⁵ For some plants, however, these rates seem certain to pose a serious problem. For example, forest understory plants re-invading formerly plowed lands in the northeastern United States migrated into new territory at approximately 0.01 km per decade (Matlack, 1994; see also Brunet and Von Oheimb, 1998), close to 1,000 times slower than the migration rate that global warming might require. An additional concern is that the existing plants at a site might persist for a relatively long period, and although performing at a physiological sub-optimal level, will remain robust enough to make invasion by other plants difficult. Existing plant communities often are quite resistant to invasion, and in the absence of large disturbance events, community-level changes may be delayed for many decades (Pitelka et al., 1997).

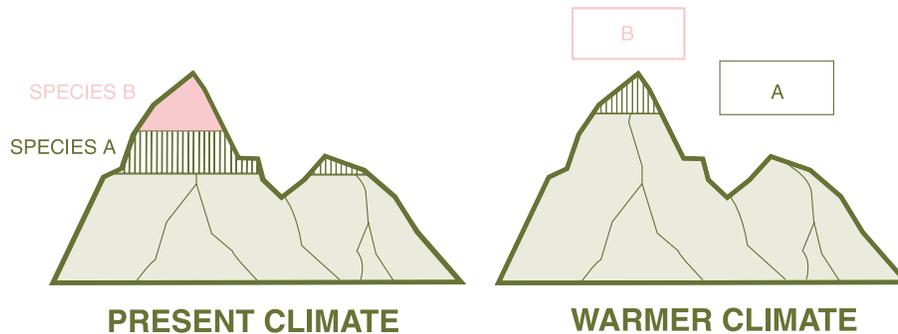
Thus, depending on its rate, global warming has the potential to create a “winnowing” or “filtering” effect similar to the reduction in biodiversity sometimes observed during human development. An example of a well-known similar effect is provided by the colonization of abandoned fields in agricultural areas. Because these fields appear infrequently and often at considerable distances from one another, the pool of potentially colonizing plants has been narrowed to those plants that are able to disperse rapidly over long distances, resulting in a recognizable “old-field flora” (Matlack, 1994). A similar effect could occur under global warming. As the climate shifts, climatically-sensitive plants will eventually die out, and only a subset of the potential pool of incoming plants may actually migrate sufficiently quickly to keep up with the shifting climate. Thus, plant communities could become progressively composed of the more climatically-tolerant and fast-moving species, especially if the warming is rapid. This change in plant communities, especially tree communities, is of considerable concern. Solomon and Kirilenko (1997) investigated the potential effect of this filter on carbon storage. They modeled two scenarios: one in which trees were perfectly able to keep up with global warming and another in which they were not able to colonize new sites at all. In the perfect migration scenario, the climate associated with a doubling of atmospheric CO₂ concentrations resulted in a 7 to 11 percent increase in global forest carbon, whereas under zero migration, a 3 to 4 percent decline in forest carbon was observed. Sykes and Prentice (1996) also investigated these two scenarios in more detail for a site in southern Sweden. Compared to perfect migration, zero migration resulted in fewer tree species and lower forest biomass.

A related concern is the possibility that different parts of the ecosystem will respond to the warming at different rates, hence altering the combination of conditions that a species might require. For example, a study by Martin (in press) in high elevation forests of Arizona showed the potentially negative impact of novel combinations of climate and vegetation on breeding birds. Small valleys in the study area provided a gradient in moisture conditions, from dry locust and oak forests on the upper slopes to wet maple and aspen forests on the lower slopes. Some bird species nested at the drier end, whereas others nested at the wetter end. Martin observed that in unusually wet or dry years, the moisture gradient shifted up or down the slope. In these years, breeding birds were faced with a choice: follow the moisture gradient, or stay in the right type of forest (which did not move from one year to the next). He observed that the birds followed the moisture gradient instead of the tree gradient, but suffered increased nest predation as a result. The alternative, nesting in the right forest type, but the wrong climate, may have incurred physiological or foraging costs. These interacting sets of changes make predicting responses to climate change especially difficult.

Another important threat to consider is the potential for the outright loss of the cold conditions required by arctic and alpine species as depicted in Figure 3. As warming proceeds, the zone of cool climate in high latitudes and high on mountains moves higher still, reducing the area available for species that live in these areas (e.g., Delcourt and Delcourt, 1998). As warming proceeds, these habitats will progressively decrease in size, leading to populations that are more isolated and have higher probabilities of extinction over time. On mountain tops, the potential threat to biodiversity might be greatest for isolated mountain ranges, such as in the Great Basin (MacDonald and Brown, 1992), as opposed to situations such as the Rocky Mountains where the mountains exist as a continuous north-south range.

Figure 3

**Predicted Upward Movement of Species Distributions
on a Mountain Range due to Global Warming**



Schematic representation of a mountainous area showing the predicted upward movement of ecological zones due to global warming. In the present climate, species B is restricted to the top of one mountain, while A occurs at lower elevations. Under a warmer climate, suitable conditions no longer exist for B and A has moved upward. Similar reasoning can also be applied to species distributions along latitudinal gradients. Under a warmer climate, species distributions can generally be expected to shift poleward.

D. Climate Change Caught in the Act?

Several studies around the world have documented what appear to be the first signs of the effects of global warming on terrestrial ecosystems.

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These studies document the sensitivity of species and ecosystems to changes in climate, although, in most cases, it has not been clearly established that the regional climate change in fact is due to global warming. However, the changes are consistent with what is expected under global warming.

Arctic Ecosystems

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Reconstruction of past climate change from a wide variety of arctic tree-line sites around the world indicates steady warming since about 1840, with current conditions warmer than at any time in the past 300 years. Over the period 1978–1998, the area of multi-year ice in the arctic has declined by about 7 percent per decade (Johannessen et al., 1999). Changes in the extent of sea ice can be expected to influence seasonal distributions, ranges, patterns of migration, nutritional status, reproductive success, and ultimately abundance of the many arctic marine species. These include polar bears, which spend the winter on the ice pack hunting for seals, and other species associated with or dependent on sea ice, such as arctic cod, ring seals, walrus, narwhal, and beluga (Tynan and DeMaster, 1997). Near the southern

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extreme of the polar bear's range in western Hudson Bay, the breakup of the sea ice in the area has been occurring earlier and earlier. The condition of polar bears has declined significantly and females are having fewer young (Stirling et al., 1999). Recent warming in the Bering Sea is thought to be a factor behind massive declines of harbour seals and several bird species (BESIS, 1997).

The arctic is a habitat that provides abundant resources and food during its brief burst of productivity in the summer. In northern Manitoba at La Perouse Bay in the eastern arctic, the last 15 years or so have seen a steady increase in goose numbers (including both Canada and Snow Geese) under the influence of increased food availability in their winter habitat in the United States, decreases in hunting pressures, and increased protection in refuges. At the same time, the eastern arctic has been the site of a trend towards cooler early spring conditions, unlike the western arctic which has seen warmer and warmer springs. The ever-increasing goose populations are arriving at the Bay's marsh before spring has gotten underway. In response to the lack of new plant growth, the snow geese use their serrated bills to eat the roots and rhizomes of the still dormant marsh plants. The removal of marsh vegetation becomes self-reinforcing: less vegetation cover leads to increased evaporation during the increasingly hot summers, which in turn leads to increased salinity and plant mortality. The net effect has been a collapse of the normal marsh community. Shore birds, soil invertebrates, and grazing ducks were all negatively affected (Srivastava and Jefferies, 1996; Kotanen and Jefferies, 1997).

Long-term studies at Toolik Lake, Alaska in the northern foothills of the Brooks Range also indicate ongoing regional temperature increases with important potential impacts on wildlife species (Chapin et al., 1995). There, researchers used greenhouses to raise temperatures, and found that in the 9 years from 1981 through 1989, tundra species richness was reduced by 30 to 50 percent due to a loss of relatively rare species. Surprisingly, during the decade of study, Chapin et al. also observed changes in the nearby unperturbed tundra that in many ways mirrored the experimental warming. Chapin et al. suggested that the changes they observed might have important implications for browsing arctic wildlife such as caribou. The fruiting bodies of forb species that disappeared or were strongly reduced under warming are nutritionally important for caribou and are selectively grazed when they are feeding their young, a time of high energy demands on the mothers. Lichens, a critical winter food for caribou, also became less abundant in the experimental warming.

The Boreal Forest

Global warming in the high northern latitudes has been greater than elsewhere on the planet, and in response to approximately 100 years of warming, tree growth has accelerated overall. The overall increased growth in northern forests is manifested in data collected by weather satellites. These data indicate an increase in summer plant growth of approximately 7 to 14 percent above 45 degrees north latitude between 1981/1982 and 1990, apparently as a result of an increase in the length of the active growing season brought about by warmer temperatures and earlier disappearance of snow. The increased growth in North America was especially concentrated in a band extending from Alaska, southeast towards the Great Lakes, and northeast towards Labrador (Myneni et al., 1997).

Nevertheless, as revealed by the widths of tree rings at the tree-line where trees are especially sensitive to climate, this pattern of increasing tree growth may be changing. Specifically, despite warm conditions and even though tree growth has increased, the rate of tree growth during the last several decades has not matched past growth rates. One possibility is a lack of sufficient energy from the sun to fuel growth because of the northern locations and the effects of clouds. In addition, beginning in around 1970, trees became more sensitive to rainfall patterns, suggesting a role of water stress in limiting tree growth (Jacoby and D'Arrigo, 1995). This moisture stress, combined with warmer conditions that could lead to increased insect populations, could lead to severe insect outbreaks, such as the severe bark beetle infestations that have decimated several million hectares of southern Alaskan forest (Taubes, 1995).

Temperate Ecosystems

As the earth warms, warmer temperatures are expected to shift poleward, resulting in shifts of the geographic ranges of many species. Considerable evidence of these shifts in temperate forests has come from Europe, but similar effects can be expected in the temperate forests of the United States. Parmesan et al. (1999) provided the first large-scale evidence of poleward shifts of ranges. In a sample of 35 non-migratory European butterflies, 63 percent had ranges that shifted to the north by 35–240 km during this century, and only 3 percent shifted to the south. In agreement with these findings, Hill et al. (1999) documented that the speckled wood butterfly has expanded its northern margin in the United Kingdom (U.K.) substantially since 1940, and suggested that fragmentation of habitats may constrain the northward expansion of this species at its northern margin in the U.K. Bird ranges also are apparently

shifting, as evidenced from a comparison of records between 1968–1972 and 1988–1991. The northern ranges of species restricted to the southern part of the U.K. shifted significantly northward during this period, on average close to 20 km (Thomas and Lennon, 1999). These shifts in distributions are consistent with long-term warming trends in Europe and the U.K. Shifts in the timing of reproduction have been observed during the last decades, correlated with the earlier arrival of spring and presumably the earlier appearance of food supplies. Of 21 U.K. bird species that had significantly changed their laying date during the 25-year period from 1971 to 1995, 20 laid their eggs earlier (on average by 9 days) whereas only one laid its eggs later (Crick et al., 1997; see also Forchhammer et al., 1998; Crick and Sparks, 1999). Amphibians have also been spawning earlier in the year as spring temperatures in the U.K. have increased (Beebee, 1995). A recent study in southeastern Arizona has documented the same phenomenon. From 1971 to 1998, the average date by which Mexican Jays laid their first clutch of eggs moved 10 days earlier in the spring. Again, the change was associated with increasingly warm spring temperatures (Brown et al., 1999).

E. Interactions between Climate Change and Other Human Pressures

The effects of climate change on ecosystems must be considered in the context of a range of other human-caused impacts on ecosystems. Over the past 200 years, vast areas of natural vegetation in the United States have been converted to agriculture, housing, and other new land uses such that, in many parts of the country, areas of natural habitat are represented by small, isolated patches in a human-dominated landscape. The Nature Conservancy estimates that one half of the endangered plant species in the United States are already restricted to 5 populations or fewer (Pitelka et al., 1997). The associated dramatic reductions in population sizes of many species of plants and animals not only increase the risks of extinction, but also make migration more difficult because of the distances between remaining patches and the difficulties of migrating through an often inhospitable human-dominated landscape. Each further loss of a population may make migration in response to climate change more unlikely, especially if “outlier” populations are lost (i.e., populations that are relatively far from the main body of the population). These outlier populations can serve as a source of migrants and potentially greatly accelerate the migration of a species (Clark, 1998). While habitat fragmentation can be expected to reduce the rate of migration in general, there are occasional instances in which fragmentation might increase the rate. For example, a bird that carries seeds between suitable habitat patches might

carry them further if the habitat patches are farther apart. Overall, the new threat of climate change is likely to be especially damaging for ecological communities and species that have suffered the greatest losses from human development and habitat destruction and fragmentation, such as coastal wetlands, riparian forests, and native prairie.

Many terrestrial and aquatic ecosystems in the United States experience significant levels of air or water pollution. For natural ecosystems already under stress because of air or water pollution, their capacity to successfully adapt to climate change will be diminished.

Invasive exotic species are another stress that could be exacerbated by climate change. Many ecosystems in the United States already have been dramatically altered by invasive species (Mack et al., 2000). Examples include the grasslands of the Great Basin, coastal bays and estuaries, and the deciduous forests of the eastern United States, where Dutch elm disease and chestnut blight eliminated once dominant trees and changed the character of the forests. Invasive species thrive and have their most serious effects in ecosystems already disturbed by human activities. Climate change could represent a new form of disturbance to natural ecosystems and thus could provide new opportunities for invasive species to flourish and displace native species. An important feature of many invasive species is that they are effective at dispersing and have high reproductive rates. These features may enable them to colonize disturbed or vacated habitats before native species.

Climate change may pose a particular threat to U.S. Parks and Protected Areas, which in some cases are the last strongholds of certain kinds of ecosystems and species, and where ecosystems and species often are already threatened by human activities. Climate change threats include redistribution and loss of already limited habitat, increased fire frequency and risk, and increased vulnerability to invasive species and pests (Malcolm and Markham, 1997).

IV. Social Implications of Ecosystem Change

Society relies on the natural world in many direct and indirect ways (Costanza et al., 1997). An estimated 40 to 50 percent of total plant production on land is appropriated by humans, either through direct use or through modifications of landscapes that make them less productive (Vitousek et al., 1986; Pimental et al., 1997). While some 60 percent of human use comes from just a few species — rice, wheat, and corn (Wilson, 1988) — an estimated 20,000 species of plants have been used by humans as food. Ecosystems play a number of other roles that are also of high economic value, including waste disposal, plant pollination, food and pharmaceutical production from the wild, wood production, removal of chemicals from the environment, production of genetic resources to improve crop and livestock yields, ecotourism, and biocontrol of pests (see Box 1). Pimental et al. (1997) estimated that, aside from the value of crops and livestock, economic and environmental benefits from U.S. ecosystems, species, and their genetic material were worth approximately \$319 billion per year, or 5 percent of the U.S. Gross Domestic Product.

In some cases, climate change may directly influence economic returns because of effects on harvests. Examples include effects on production of timber, fish, shellfish, wild game, and livestock from rangelands. Although economic impacts are rarely calculated, many studies indicate significant potential for disruption of current harvesting practices and livelihoods. For example, based on climate modeling by the Canadian Climate Centre, Welch et al. (1998) predicted that global warming by 2050 would be sufficient to exclude sockeye salmon from the entire Pacific Ocean. Similarly, Sorenson et al. (1998) found that 11 of 12 increased temperature scenarios resulted in increased drought by the middle of the twenty-first century in the northcentral United States (due to greater water loss from plants) and led to marked declines in the numbers of ducks from close to 5 million ducks at present to 600,000 to 800,000. Many studies indicate significant shifts in forest composition and hence potential shifts in timber and non-timber forest production (e.g., Iverson and Prasad, 1998; Rehfeldt et al., 1999). Sohngen and Mendelsohn (1998) used VEMAP results in combination with an economic model of the timber industry to conclude that climate change would benefit the industry overall in the United States.⁶

Generally, highly managed ecosystems, especially those in which the production cycles are over short time frames, are more easily adapted to a changing climate. Where long-term planning is required, such as in many forestry operations, climate change has greater potential for negative effects; for example, if possible climatic shifts are ignored or if assumptions about future climate are incorrect (for example, the warming occurs more quickly than expected). In natural ecosystems, economic impacts are difficult to predict because of complex interactions among species.

Whereas the benefits of harvesting biotic resources are easily defined, other benefits of ecosystems are much more difficult to calculate because they are widespread, poorly understood, and not reflected in market prices (Oldfield, 1984). Some species may have a value or worth associated with their existence in a location. For example, in addition to their economic value, the sugar maples of Vermont are very important to many people of the state, in part because of the attractiveness of the trees (especially in fall). It may matter to people in Vermont that sugar maples might largely disappear and be replaced by oaks. Similarly, in the western United States, climate change has the potential to significantly alter the current landscapes that residents hold dear. Many people choose to situate their homes on mountain slopes at the transition between grassland and forest, i.e., where the two types mix to form a “park land” of intermixed forest and grassland. With climate warming, vegetation zones will move up in elevation and many of these areas that currently are within the transition zone between forest and grassland could eventually end up being only grassland.

One approach to providing a financial accounting of the true value of ecosystems is to use nonmarket valuation techniques (Thresher, 1981; Smith, 1993). These are techniques that attempt to value goods and services not traded in markets, for example, by determining how much people are willing to pay to use a national park. However, even where diversity in itself appears to be an economic asset, the “marginal utility” of diversity from a classic economic viewpoint is not clear (Sagoff, 1996). That is, given that a diverse array of species provides a service, it is usually not clear what economic costs might be incurred by the loss of just one or a few species. For example, high diversity appears to be important in several of the economic roles that ecosystems play, such as in soil formation, bioremediation, biotechnological gene transfer, control of pests by natural enemies, pollination, and identification of plant-based drugs and medicines (Pimental et al., 1997). However, the marginal economic costs associated with progressive losses of biodiversity or ecosystem functioning — perhaps through the filtering effect of climate change discussed in Section III.C — are unknown.

While continued efforts need to be made to define the economic value of ecosystems, it should be kept in mind that valuation of natural resources based solely on contributions to monetary gain can be expected to lead to a steady erosion in environmental quality (Krutilla, 1967; Norgaard, 1994). The value of ecosystems must also be considered in a broader context, including moral, aesthetic, and cultural values (Kellert, 1984; Sagoff, 1996). An analogy with the Endangered Species Act is illustrative. The Act explicitly prohibits the use of economic impacts in setting acceptable levels of extinction. From this broader perspective of the moral and aesthetic value of diversity, climate change has the potential to worsen what is already perceived by most scientists to be a biodiversity crisis. Many scientists believe that the rate of extinctions has grown exponentially since the fourteenth century (Soulé, 1991), and it currently appears to be at least 100 times, and perhaps as high as 10,000 times, higher than the background pre-human rate (Wilson, 1988; May et al., 1995; Pimm et al., 1995).

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V. Adaptation

The degree to which species can adapt to climate change is inherently limited. As defined by the IPCC (1996a), “adaptability” refers to: “...the degree to which adjustments are possible in practices, processes, or structures of systems to projected or actual changes of climate. Adaptation can be spontaneous or planned, and can be carried out in response to or in anticipation of changes in conditions.”

Organisms have evolved various mechanisms to track the climatic conditions under which they are able to live and reproduce. Thus, in response to climate change, they will adapt “autonomously” — that is, by their own devices. This ability is limited, however, because in the absence of significant evolutionary change (which typically requires tens of thousands of years or more), species are dependent on their built-in flexibility and capabilities to respond to climate change. If suitable habitat conditions disappear, or shift in position faster than populations can respond, extinctions will occur (Malcolm et al., 1998). The result will be less diverse ecosystems, and potentially, ecosystems that fail to perform the diverse set of functions that they once did. Therefore, it is important to emphasize that evolutionary change will not be an important mechanism by which natural species can accommodate climate change, at least within a matter of a few centuries. The only types of species in which true evolutionary change could occur are those with very short life cycles — a year or less. Thus, it is the weedy plants and pest organisms that would be most likely to evolve, whereas species that are valued the most often have longer life cycles and will be unable to evolve.

Given these innate limitations, an important strategy for allowing organisms to respond to their full potential is to maintain the habitats that they currently live in — that is, to maintain overall ecosystem structure and species composition. This can be accomplished by reducing fragmentation, loss and degradation of habitat, increasing connectivity among habitat blocks and fragments, and reducing external anthropogenic environmental stresses (Markham and Malcolm, 1996). Thus, adaptation to climate change should benefit from existing strategies to conserve biodiversity and protect natural ecosystems. Various general strategies to conserve biodiversity include establishment and maintenance of viable

protected areas networks, management of wild populations outside of protected areas, and the maintenance of captive populations. Some characteristics of protected area networks that are thought to improve their viability in the face of a changing climate include:

- redundancy of populations;
- maximization of reserve connectivity, size, and number;
- protection of areas that offer significant heterogeneity in topography, habitat, and microclimate; and
- development of biodiversity-friendly management schemes in the landscapes surrounding reserves (Markham and Malcolm, 1996; Malcolm and Markham, 1997).

Techniques to accomplish the latter include reduction of fragmentation of natural habitats and establishment of corridors that function as habitat rather than as mere transit lanes (Simberloff et al., 1992). The potential for climate change should be explicitly incorporated into decision-making concerning the selection of appropriate areas for conservation.

In addition to maximizing the potential for nature to take its own course, adaptive responses may include the active management of natural ecosystems, for example, by assisting plant species to migrate. Indeed, the rapidity of the coming change suggests that these responses will be required. However, the analogy that ecosystems can be “managed” in the same way that much simpler human-designed industrial systems can, is misleading and dangerous (Walker and Steffen, 1997). Natural ecosystems are more complex than human systems and often react to disturbances in unanticipated ways. An example of this difficulty is presented by what would appear to be a simple task: the reintroduction of a single plant species into a part of its former range (see Allen, 1994). Of 29 reintroduction projects in California in the past decade, 10 failed to result in a new population becoming established. Similarly, in a 1991 study by the British Nature Conservancy Council, only 22 percent of 144 species reintroductions were deemed successful and more than half appeared to have failed. Successful reestablishment of functioning ecosystems, which might include establishment of self-sustaining populations, pollinators, mycorrhizal fungi, seed dispersers, nutrient cycles, and hydrology, is much less likely (Allen, 1994).

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VI. Conclusions

1. Climate is the single most important factor determining the distributions of major vegetation types and individual species. This tenet is a fundamental principle of ecology and has been recognized since the birth of the science. Evidence from paleoecological data documents that past variations in climate have resulted in major shifts in the distribution of species and the species composition of ecosystems.

2. Ecological models predict that, if climate changes as proposed by climate models, the distributions of major vegetation zones and species will be significantly altered. In general, distributions will shift northward in the United States, with more complex patterns of change in the topographically complex regions of the West. Certain types of vegetation may disappear entirely from the United States or be greatly reduced in extent. The geographic area of arctic, alpine, and estuarine ecosystems, in particular, may decline, resulting in reduced populations of the organisms that inhabit these ecosystems.

3. Climate change will affect the functioning of ecosystems and the goods and services that they provide. Plant productivity is very sensitive to climate change and will certainly change as climate changes. Model projections for the United States as a whole indicate that under a doubling of atmospheric CO₂ concentrations, the change in productivity could range from a minor decrease to a large increase. Regional patterns are far more complex, with some areas likely to experience decreases in plant productivity.

4. Climate change will affect the species composition of ecosystems, both as a function of the magnitude and rate of the change. As climatic zones shift, the species composition of ecosystems will shift, depending on the ability of organisms to tolerate the changed climate and colonize climatically suitable areas. The faster and more extreme the shift, the more likely are reductions in species diversity, through selective favoring of climatically tolerant and rapidly colonizing species.

5. There still is a high level of uncertainty concerning the effects of climate change on ecosystem properties and processes. This uncertainty arises in part from not knowing exactly how climate will change, especially with respect to precipitation and regional patterns of change. In addition, current understanding of the functioning of ecosystems and their component parts is insufficient for making precise projections concerning the ecological effects of a specified change in climate. This lack of understanding not only makes it difficult to predict ecosystem responses, but also compromises the ability to manage ecosystems in order to mitigate, minimize, or ameliorate the effects of climate change.

6. Climate change cannot be viewed in isolation but rather must be considered in the context of other human-caused stresses on ecosystems, such as air pollution, water pollution, habitat destruction and fragmentation, and invasive species. In many, but not all cases, interactions with other stresses are likely to exacerbate the effects of climate change (and vice versa). As a result, strategies for reducing the impacts of climate change on ecosystems should focus on reducing existing pressures.

7. Many of the impacts of climate change on ecosystems and biodiversity have implications for human society. These impacts include changes in harvest levels from natural and managed ecosystems, reductions in diversity and attendant reductions in goods and services, and aesthetic and cultural impacts of regional shifts and losses of biological resources.

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Endnotes

1. Future Pew Center reports will cover climate change impacts on aquatic ecosystems and forests.

2. The set of climate models used in VEMAP was different from that used by Wigley (1999), hence the range of average temperature increases is different (3.0°C–6.7°C for VEMAP vs. 2.2°C–5.2°C in Wigley). Note that this range represents projections for the continental United States and thus is different from the range of projected warming for the world as a whole.

3. Direct effects of elevated CO₂ on agricultural systems are discussed in a previous Pew Center report (Adams et al., 1999).

4. A previous Pew Center report addressed the issues of land use and carbon sequestration in greater detail (Schlamadinger and Marland, 2000).

5. In approximately 40 years after its arrival in western North America in about 1880, cheatgrass had occupied most of its range of 200,000 km² (Mack, 1986). Assuming a circular range, a 40-year period to traverse the radius gives an estimated migration rate of 6,300 m/yr. Weber (1998) found that as two goldenrod species (Soldago) invaded Europe, diameters of their geographic ranges increased from 400 to 1,400 km between 1850 and 1875 and from 1,400 to 1,800 km between 1875 and 1990 (see his Figure 4). Respective migration rates assuming a circular range expanding evenly outward are approximately 20,000 and 1,740 m/yr.

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6. Sohngen and Mendelsohn (1998) made several simplifying assumptions that might influence this conclusion. For example, although ecosystems are sensitive to changes in weather extremes, the authors relied on long-term weather averages. In addition, as discussed in Section III.A, the VEMAP models that they relied upon generally did not include the effects of natural fires, herbivores, or disease, which can have major effects on vegetation patterns. The authors also did not consider the possibility that the establishment of timber trees at new sites might significantly lag behind the rate of climate change or that appropriate species might fail to establish at all (see Section III.C). On intensively managed lands, they assumed that silvicultural practices would succeed in rapidly establishing species adapted to the new conditions, which will not always be the case. Low intensity lands were assumed to regenerate to appropriate species after at most a 10–30 year lag (depending on the species). A final caveat concerns the magnitude of warming. Sohngen and Mendelsohn assumed that policy would stabilize climate at the equilibrium expected under a doubling of atmospheric CO₂ concentrations. Effects beyond a doubling of CO₂ were not investigated.

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