

ESA Report

ECOLOGICAL PRINCIPLES AND GUIDELINES FOR MANAGING THE USE OF LAND¹

V. H. DALE,^{2,11} S. BROWN,^{3,12} R. A. HAEUBER,^{4,13} N. T. HOBBS,⁵ N. HUNTLY,⁶ R. J. NAIMAN,⁷
W. E. RIEBSAME,⁸ M. G. TURNER,⁹ AND T. J. VALONE^{10,14}

²Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831-6036 USA

³Department of Natural Resources and Environmental Sciences, University of Illinois, Champaign, Illinois 61820 USA

⁴Sustainable Biosphere Initiative, Ecological Society of America, Washington, D.C. 20006 USA

⁵Colorado Division of Wildlife and Natural Resource Ecology Laboratory, Colorado State University,
Fort Collins, Colorado 80523 USA

⁶Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209-8007 USA

⁷College of Ocean and Fishery Sciences, University of Washington, Seattle, Washington 98195-2100 USA

⁸Department of Geography, University of Colorado, Boulder, Colorado 80309 USA

⁹Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA

¹⁰Department of Zoology, California State University, Northridge, California 91330-8303 USA

Abstract. The many ways that people have used and managed land throughout history has emerged as a primary cause of land-cover change around the world. Thus, land use and land management increasingly represent a fundamental source of change in the global environment. Despite their global importance, however, many decisions about the management and use of land are made with scant attention to ecological impacts. Thus, ecologists' knowledge of the functioning of Earth's ecosystems is needed to broaden the scientific basis of decisions on land use and management. In response to this need, the Ecological Society of America established a committee to examine the ways that land-use decisions are made and the ways that ecologists could help inform those decisions. This paper reports the scientific findings of that committee.

Five principles of ecological science have particular implications for land use and can assure that fundamental processes of Earth's ecosystems are sustained. These ecological principles deal with time, species, place, disturbance, and the landscape. The recognition that ecological processes occur within a *temporal* setting and change over time is fundamental to analyzing the effects of land use. In addition, individual *species* and networks of interacting species have strong and far-reaching effects on ecological processes. Furthermore, each *site* or region has a unique set of organisms and abiotic conditions influencing and constraining ecological processes. *Disturbances* are important and ubiquitous ecological events whose effects may strongly influence population, community, and ecosystem dynamics. Finally, the size, shape, and spatial relationships of habitat patches on the *landscape* affect the structure and function of ecosystems. The responses of the land to changes in use and management by people depend on expressions of these fundamental principles in nature.

These principles dictate several guidelines for land use. The guidelines give practical rules of thumb for incorporating ecological principles into land-use decision making. These guidelines suggest that land managers should: (1) examine impacts of local decisions in a regional context, (2) plan for long-term change and unexpected events, (3) preserve rare landscape elements and associated species, (4) avoid land uses that deplete natural resources, (5) retain large contiguous or connected areas that contain critical habitats, (6) minimize the introduction and spread of nonnative species, (7) avoid or compensate for the effects of development on ecological processes, and (8) implement land-use and management practices that are compatible with the natural potential of the area.

Decision makers and citizens are encouraged to consider these guidelines and to include ecological perspectives in choices on how land is used and managed. The guidelines suggest actions required to develop the science needed by land managers.

Key words: conservation; disturbance; ecological processes; ecosystem function; environmental policy; keystone species; land management; land use, ecological principles and guidelines; landscape; nonnative species; planning; settlement patterns.

Manuscript received 15 May 1998; revised 1 March 1999; accepted 31 May 1999; final version received 1 September 1999.

¹ This article is the Report of the Ecological Society of America Committee on Land Use (V. H. Dale, chair). For a copy of this 32-page report, available for \$4.75, or for further information, contact The Ecological Society of America, 1707 H Street, N.W., Suite 400, Washington, DC 20006.

¹¹ E-mail: vhd@ornl.gov

¹² Present address: Winrock International, Arlington, Virginia 22209 USA.

¹³ Present Address: U. S. Environmental Protection Agency, Clean Air Markets Division, S01 3rd Street, N.W., Washington, DC 20001 USA.

¹⁴ Present address: Department of Biology, St. Louis University, St. Louis, Missouri 63103 USA.

INTRODUCTION

Wake, now, my vision of ministry clear; Brighten my pathway with radiance here; Mingle my calling with all who will share; Work toward a planet transformed by our care.

T. J. M. Mikelson, 1936

The words of the Irish hymn by Mikelson have been applied literally to the earth. During the past few millennia, humans have emerged as the major force of change around the globe. The large environmental changes wrought by our actions include modification of the global climate system, reduction in stratospheric ozone, alteration of Earth's biogeochemical cycles, changes in the distribution and abundance of biological resources, and decreasing water quality (Meyer and Turner 1994, IPCC 1996, Vitousek et al. 1997, Mahlman 1997). However, one of the most pervasive aspects of human-induced change involves the widespread transformation of land through efforts to provide food, shelter, and products for our use. Land transformation is perhaps the most profound result of human actions because it affects so many of the planet's physical and biological systems (Kates et al. 1990). In fact, land-use changes directly impact the ability of Earth to continue providing the goods and services upon which humans depend.

Unfortunately, potential ecological consequences are not always considered in making decisions regarding land use. Moreover, the unique perspective and body of knowledge offered by ecological science rarely are brought to bear in decision-making processes on private lands. The purpose of this paper is to take an important step toward remedying this situation by identifying principles of ecological science that are relevant to land-use decisions and by proposing a set of guidelines for land-use decision making based on these principles (Fig. 1). This paper fulfills this purpose through four steps. (1) It describes the conceptual and institutional foundations of land-use decision making, outlining the implementation of U.S. land-use decisions. (2) It identifies (a) ecological principles that are critical to sustaining the structure and function of ecosystems in the face of rapid land-use change and (b) the implications of these principles for land-use decision making. (3) It offers guidelines for using these principles in making decisions regarding land-use change. Finally, (4) it examines key factors and uncertainties in future patterns of land-use change. Throughout, the paper offers specific examples to illustrate decision-making processes, relevant ecological principles, and guidelines for making choices about land use at spatial scales ranging from the individual site to the landscape.

The paper focuses on the United States, which some may see as parochial; however, the incredible variety

of political, economic, social, and cultural institutions encountered throughout the world make a thorough comparative study impossible in a single paper. More importantly, while the paper concentrates on land-use decisions in the United States, the principles and guidelines it describes are applicable worldwide.

In undertaking this paper, the Land Use Committee of the Ecological Society of America (ESA) continues an ongoing effort by the Society to marshal the resources and knowledge of the ecological-science community in understanding and resolving critical environmental-policy and resource-management issues. In 1991, for example, the Sustainable Biosphere Initiative (Lubchenco et al. 1991) established the priority research areas that must be explored if ecologists are to contribute in maintaining Earth's life-support systems. Similarly, the ESA Report on the Scientific Basis of Ecosystem Management (Christensen et al. 1996) focused on the application of ecological science in managing ecological systems for extractive uses. Our report continues that tradition, offering relevant ecological principles for making decisions regarding human actions that change the land from one category of use to another (e.g., from forests to agriculture or from agriculture to housing subdivisions).

Trends and patterns of land-use change

Changes in the cover, use, and management of the land have occurred throughout history in most parts of the world as population has changed and human civilizations have risen and fallen (e.g., Perlin 1989, Turner et al. 1990). Over the centuries two important trends are evident: the total land area dedicated to human uses (e.g., settlement, agriculture, forestry, and mining) has grown dramatically, and increasing production of goods and services has intensified both use and control of the land (Richards 1990). At the end of the 20th century, much of Earth's habitable surface is dedicated to human use, mostly for production of food and fiber. Some is used for conservation, but even that area is mapped, zoned, and controlled.

Forests and grasslands, in particular, have undergone large changes (Houghton 1995). These changes have occurred at different times in various parts of the world. It is estimated that, between 1700 and 1980, the area of forests and woodlands decreased globally by 19% and grasslands and pastures diminished by 8% while world croplands increased by 466% (Richards 1990). Furthermore, the pace of change has accelerated, with greater loss of forests and grasslands during the 30 yr from 1950 to 1980 than in the 150 yr between 1700 and 1850. Global croplands increased more since World War II than in the entire 19th and early 20th centuries. Many centuries ago, intensive use of European forests produced construction materials, fuelwood, and agri-

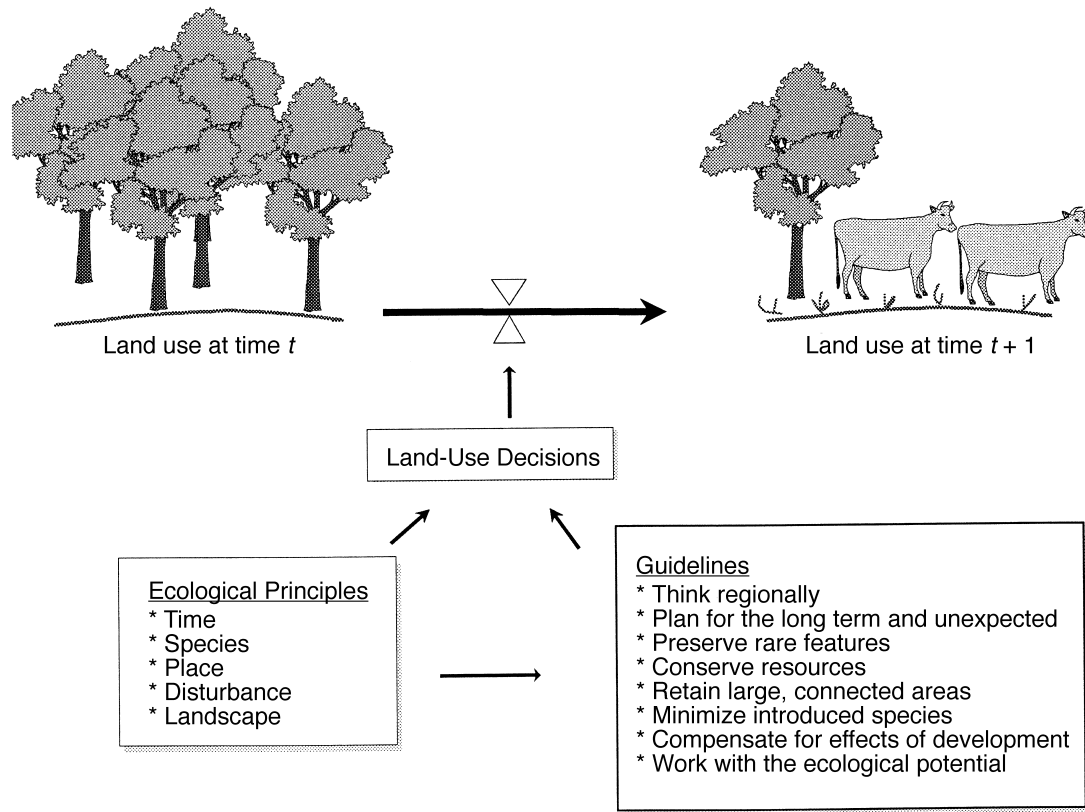


FIG. 1. A roadmap to this paper shows that ecological principles relating to land use are developed into guidelines for land managers. These guidelines can inform land-use decisions so that land uses in the future benefit from ecological knowledge.

cultural lands (Perlin 1989). More recently, forest area in midlatitude countries has stabilized or increased as fossil fuels were substituted for wood and as agriculture intensified. Forests and grasslands in the tropical regions of the world currently are experiencing the highest rates of change that have ever been recorded for large regions (Houghton et al. 1991, FAO 1993, 1996, Richards and Flint 1994).

Similar trends in land-use change occurred in the United States as North America was colonized and settled by Europeans. It is seldom recognized that the historical rates of deforestation in some locations of the continental United States were as great as those in the tropics today (see Table 1). During the late 1800s, for example, deforestation in Illinois peaked at $>2.4\%/yr$, a rate similar to those experienced by Costa Rica and Peninsular Malaysia in the past few decades (Iverson et al. 1991). Between 1860 and 1978, roughly 1.6 million km^2 of forests and grasslands were converted to croplands in North America. In the United States, about 50 000 km^2 of forest land were cleared for farms before 1850, and an additional 800 000 km^2 came under the

plow between 1850 and 1909 (Williams 1990). The United States is an exception to the recent stabilization of forest area in developed countries. Its forested area decreased by about another 50 000 km^2 between 1950 and 1992 (U.S. Department of Commerce, Bureau of the Census 1975, 1991, 1996). Remaining forests are generally younger and thus growing rapidly. Although many agricultural lands reverted to forests in the eastern United States, the continued decline in the nation's forest area reflects other land conversion, such as expansion of urban and suburban areas.

The present distribution of major land uses in the contiguous United States (Fig. 2) reflects a complex pattern of historical conversion of lands to human-dominated lands. Today, the U.S. government owns 263 million ha or 31% of this land area. About 67% of the land in the contiguous United States is privately held, and another 2% is owned by state or local governments (together making up the nonfederal lands). Developed nonfederal lands have increased by 18% in the last decade to 92 million hectares or 4.4% of the total area.

Box 1. Definition of Terms

Land cover is the ecological state and physical appearance of the land surface (e.g., closed forests, open forests, or grasslands) (Turner and Meyer 1994). Change in land cover converts land of one type of cover to another, regardless of its use. Land cover is also affected by natural disturbances, such as fire and insect outbreaks, and subsequent changes through succession.

Land use refers to the purpose to which land is put by humans (e.g., protected areas, forestry for timber products, plantations, row-crop agriculture, pastures, or human settlements) (Turner and Meyer 1994). Change in land use may or may not cause a significant change in land cover. For example, change from selectively harvested forest to protected forest will not cause much discernible cover change in the short term, but change to cultivated land will cause a large change in cover.

Land management is the way a given land use is administered by humans. Land management (such as clear-cut vs. selective-cut harvesting, lengthening or shortening forest rotation cycles, conventional-till vs. no-till agriculture, and irrigated vs. rain-fed agriculture) can affect ecological processes without changing the basic land use.

Ecological sustainability is the tendency of a system or process to be maintained or preserved over time without loss or decline. For instance, sustainable forestry refers to forest-management practices that maintain forest structure, diversity, and production without long-term decline or loss over a region. Land use could be sustainable locally over the long term based on external subsidies from other land areas, but this practice would result in an inevitable loss from the system providing the subsidies and thus would not be seen as sustainable when viewed at the larger scale. Sustainability is widely regarded as economically and ecologically desirable; in the ultimate sense, it is the only viable long-term pattern of human land use.

Land-use dynamics refers to the changes in patterns of land use by humans over time. These changes are strongly influenced by human population density and the infrastructures that humans establish and by many aspects of lifestyle and standard of living.

Biodiversity refers to the variety of life and ecological systems at scales ranging from populations to landscapes (Franklin 1993). The numbers and kinds of plants, animals, and other organisms is a common definition of biodiversity (i.e., species richness), but the concept of diversity of biological forms and functions extends to genes, habitats, communities, and ecosystems (Franklin 1993). Diversity at all of these levels is of ecological value. It is unlikely that species diversity could be maintained without habitat and ecosystem diversity, and it is unlikely that essential services of nature could be maintained in the absence of diversity at all of these levels.

Ecosystem management is the process of land-use decision making and land-management practice that takes into account the full suite of organisms and processes that characterize and comprise the ecosystem and is based on the best understanding currently available as to how the ecosystem works. Ecosystem management includes a primary goal of sustainability of ecosystem structure and function, recognition that ecosystems are spatially and temporally dynamic, and acceptance of the dictum that ecosystem function depends on ecosystem structure and diversity. Coordination of land-use decisions is implied by the whole-system focus of ecosystem management.

Settlement is the occupation of land by humans, typically referring to patterns of residential use, from dispersed to concentrated, along a continuum from rural to village to suburb to city. The term may also include infrastructure and commercial land-use patterns. Types of settlement include urbanization, suburbanization, rural agriculture, and rural subdivision. Settlement often includes simplification of the landscape; modification of disturbance patterns; changes in soil and water quantity and quality; and altered movement of nutrients, organisms, and other elements of ecological systems. Changes through settlement can be dramatic, such as paving over land to construct a shopping mall and parking lots, or less drastic, such as fragmenting the landscape by subdividing agricultural land into 4-ha homesites.

Habitat fragmentation is the alteration of previously continuous habitat into spatially separated and smaller patches. Habitat fragmentation can and often does result from human land-use dynamics, including forestry, agriculture, and settlement, but also can be caused by wildfire, wind, flooding, outbreaks of herbivores or pathogens, and many other disturbances. Suburban and rural development and subdivision commonly change patterns of habitat fragmentation of natural forests and grasslands as a result of adding fences, roads, or driveways and from individual decisions on land management and landscaping. Human activities can both decrease and increase fragmentation.

TABLE 1. Comparison of recent deforestation rates in the tropics and conversion of forest and prairie in Illinois during the settlement period.

Location	Land cover	Initial		Final		Forest cleared per year (%)
		Date	Area (ha)	Date	Area (ha)	
Rondônia, Brazil	Forest	1978	239 800	1987	208 800	1.47
Malaysia	Forest	1972	48 970	1982	36 870	2.47
Costa Rica	Forest	1940	34 210	1983	8 710	1.73
Illinois, USA	Forest	1820	55 870	1870	24 290	1.13
	Forest	1870	24 290	1923	90	0.87
	Prairie	1830	87 550	1860	10	3.33

Source: Iverson 1991.

Thus, use and management of private land is a focus of this report.

The area of all lands being farmed continued to increase by a factor of almost five from the mid-1800s to 1950 (Fig. 3). Since 1950, however, the area of croplands has declined. In New England and the Middle Atlantic states, the first regions settled, agricultural lands have steadily declined since the mid-1800s, as has the number of farms; however, the average size of farms has increased slightly since 1950 (Fig. 3). In the Pacific and Mountain states, the area of farmland increased steadily for ~100 yr from 1850; it has declined slightly since then. The number of farms in the western states has been similar to the number in the northeast, but the western farms have been ~3–9 times larger in area than northeast farms and 2–3 times the national average (Fig. 3B).

Farms in the United States not only are getting larger but also are becoming more intensively managed. For example, the area under irrigation has increased since the late 19th century, with a sharp increase after 1940 (mostly in western states). The amount of water applied rose during the 1930s and 1940s; since then, it has declined gradually (U.S. Department of Commerce,

Bureau of the Census 1975, 1991, 1996). From 1900 to 1950, farmland area in the western states also increased steeply (Fig. 3A). Application of chemicals (such as insecticides) to the land increased between 1945 and 1989 (Pimentel et al. 1992), and fertilizer use, particularly that of nitrogenous fertilizers, increased dramatically from the 1940s to the late 1980s (U.S. Department of Commerce, Bureau of the Census 1975, 1977, Kates et al. 1990, Vitousek et al. 1997).

While human activities like farming result in land transformation over great spatial extent, few alterations of the land surface are as profound as human settlement (Douglas 1994). Globally, only a relatively small amount of land conversion takes place through urbanization and suburbanization. However, the increase in human population, especially in settlements, is gaining momentum in the United States (Fig. 4) and worldwide (Lugo 1991). In 1900, only 14% of the world's population lived in urban communities (Douglas 1994). But 38% of the global population was urban by 1975, and 45% was by 1995; that figure is projected to increase to 61% by 2025 (WRI 1997). In the decade from 1982 to 1992, 2.1 million ha of forest land, 1.5×10^6 ha of cultivated cropland, 0.9 million ha of pasture

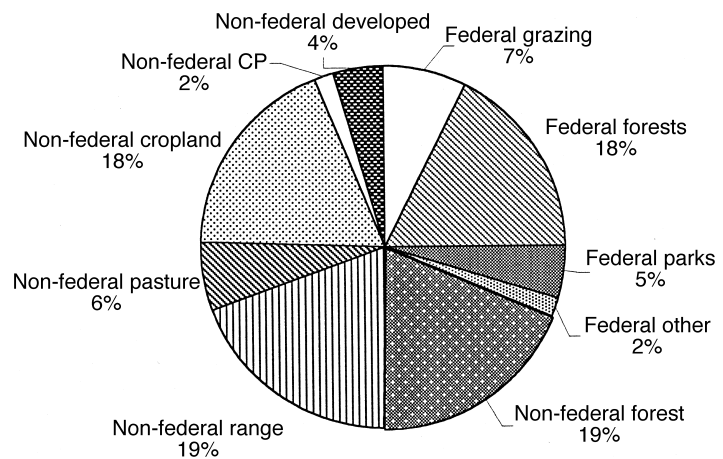


FIG. 2. Land use and ownership in the contiguous United States. Data are from the U.S. Department of Agriculture, Soil Conservation Service (1992). "CP" refers to conservation programs.

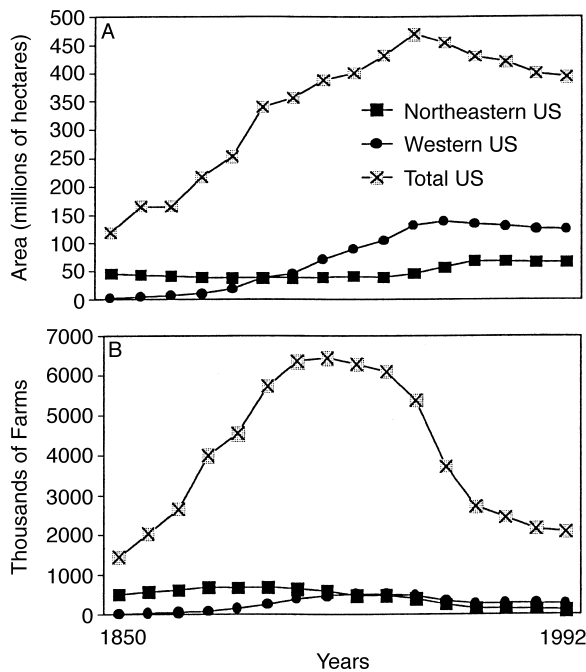


FIG. 3. Trends in the (A) area of farmland and (B) number of farms for the whole United States, and to show contrasting regions, the northeast (northeastern and mid-Atlantic states), and the west (mountain and Pacific states). Data are from the U.S. Department of Commerce, Bureau of the Census, 1975, 1977, 1991, 1996.

land, and 0.8 million ha of rangeland came under urban uses in the United States (WRI 1997). The same pattern of urbanization occurs in the developing world as well. In many developing countries, urban-population growth rates outstripped rural-population growth rates between 1990 and 1995 (WRI 1997). The impacts of human population growth might be even greater than they are today if the population were dispersed rather than concentrated in cities.

The major anthropogenic causes of change in land cover and land use include population and associated infrastructure; economic factors, such as prices and input costs; technological capacity; political systems, institutions, and policies; and sociocultural factors, such as attitudes, preferences, and values (Kates et al. 1990, Liu et al. 1993, Turner et al. 1993, Riebsame et al. 1994, Diamond and Noonan 1996). Human-population growth can be considered an ultimate cause for many land-use changes. However, population expansion is affected by many factors, such as political dynamics and policy decisions that influence local and regional trends in suburbanization, urbanization, and colonization. Moreover, local demography and variability in per capita resource consumption can modify the effects of population. In Brazil, for example, one of the highest

rates of deforestation currently occurs in the state of Rondônia, where a high rate of land-cover change results from road establishment and paving and government policies that have allowed colonists to immigrate, clearing forests so farms can be established. The rate of natural-resource exploitation also depends on technological advances in resource extraction and enhancement such as logging, mining, hydroelectric power, fertilizers, pesticides, and irrigation. The relative importance of these factors varies with the situation and the spatial scale of analysis.

Challenges of ecologically sustainable land use

A critical challenge for land use and management involves reconciling conflicting goals and uses of the land. The diverse goals for use of the land include resource-extractive activities, such as forestry, agriculture, grazing, and mining; infrastructure for human settlement, including housing, transportation, and industrial centers; recreational activities; services provided by ecological systems, such as flood control and water supply and filtration; support of aesthetic, cultural, and religious values; and sustaining the compositional and structural complexity of ecological systems. These goals often conflict with one another, and difficult land-use decisions may develop as stakeholders pursue different land-use goals. For example, conflicts often arise between those who want to extract timber and those who are interested in the scenic values of forests. Local vs. broad-scale perspectives on the benefits and costs of land management also provide different views of the implications of land actions. Understanding how land-use decisions affect the achievement of these goals can help achieve balance among the different goals. The focus of this paper is on the last goal: sustaining ecological systems, for land-use decisions and practices rarely are undertaken with ecological sustainability in mind. Sustaining ecological systems also indirectly supports other values, including ecosystem services, cultural and aesthetic values, recreation, and sustainable extractive uses of the land.

To meet the challenge of sustaining ecological systems, an ecological perspective must be incorporated into land-use and land-management decisions. Specifying ecological principles and understanding their implications for land-use and land-management decisions are essential steps on the path toward ecologically based land use. The resulting guidelines translate theory into practical steps for land managers. Ecological principles and guidelines for land use and management elucidate the consequences of land uses for ecological systems. Thus, a major intent of this paper is to set forth ecological principles relevant to land use and management and to develop them into guidelines for use of the land.

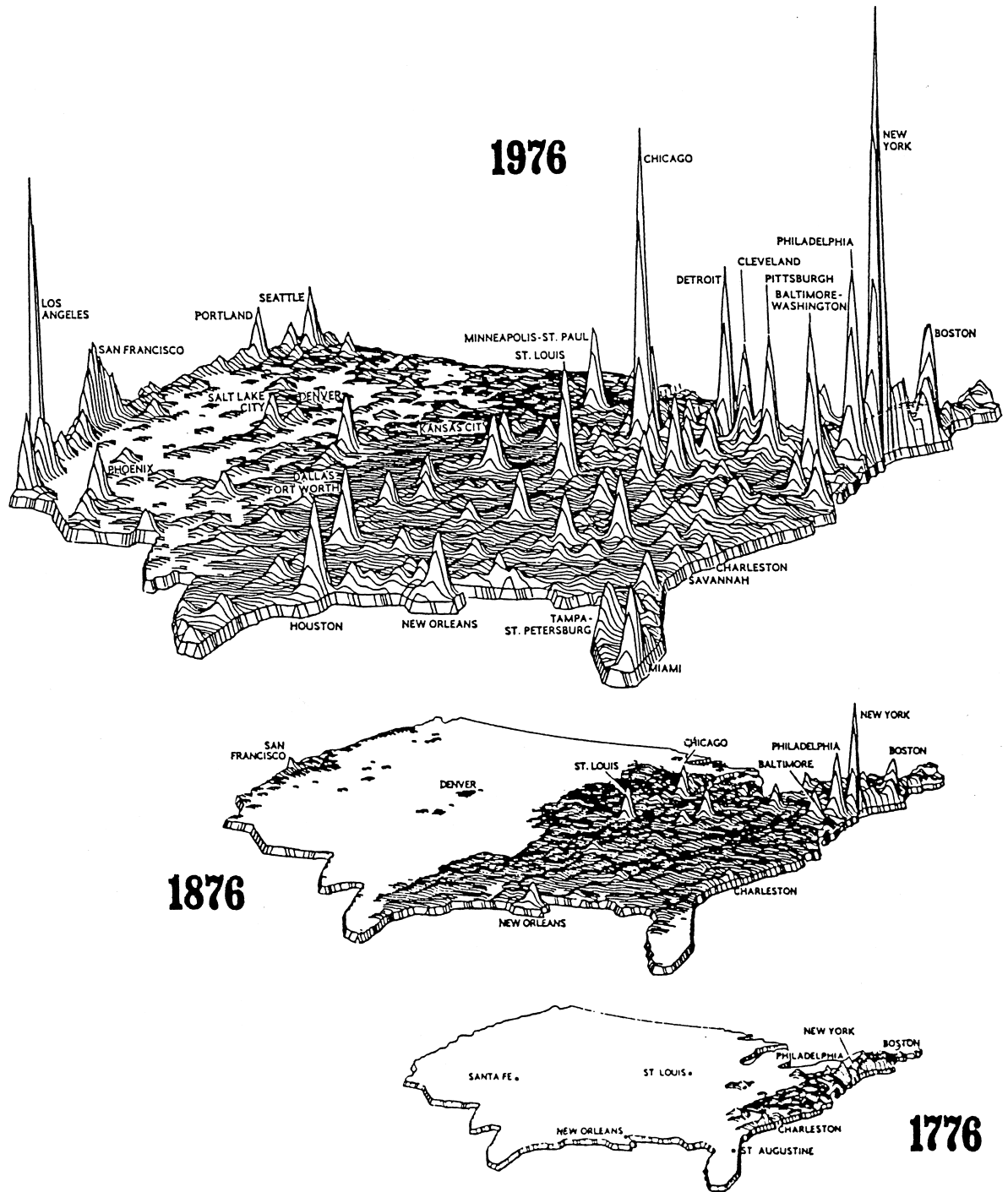


FIG. 4. Changes in the post-European settlement population density in the United States. The figure shows population density maps for 1776, 1876, and 1976, generated by Massachusetts Institute of Technology (from National Geographic, July 1976; used with permission of the National Geographic Society).

TABLE 2. Decision-making levels in the United States and examples of their land-use management powers, both regulatory and nonregulatory.

Powers	Federal	State	Local
Direct regulatory	Clean Water Act Endangered Species Act National Flood Insurance Program Surface mining reclamation Wetlands/Waterways Reclamation Act	State endangered-species acts Growth-management statutes Regulation and permitting (e.g., siting power plants, landfills, reservoirs, and mines) Programs (e.g., Coastal Zone Management)	Land-use zoning (e.g., lot size, housing density, structural dimensions, and landscaping) Agricultural land-use regulations Stormwater management
Indirect regulatory	Tax policy (e.g., estate taxes and home-mortgage deduction) Clean Air Act Transportation funding and development Agricultural programs (e.g., Conservation Reserve Program and Farmland Protection Program) Subsidies (e.g., gasohol program, land and production credit, and crop insurance)	Property-tax exemptions (e.g., for farmland or commercial property) Transportation policy Economic-development programs	Property-tax rates Water-use ordinances Local service placement and development (e.g., water and sewer systems, schools, and roads)
Management of publicly owned lands	Land-use planning (e.g., national parks, national forests, and BLM properties) National Wilderness Act Wild and Scenic Rivers Act Siting and design of roads and other facilities	State parks and forests State roads and rights of way Regulation of mining and reclamation activities	Municipal parks and recreation areas County roads and rights of way Green-space systems Greenways

LAND-USE DECISION MAKING IN THE UNITED STATES

The organization of government in the United States is based on the concept of jurisdiction: the relationships among spatial area, the discretion of citizens, and the authority of the government within that area. The importance of jurisdiction in organizing government makes it impossible to separate geography from law, and this tight coupling is particularly evident in the ways that land-use decisions are made (Platt 1996).

Jurisdictions for land-use decisions in the United States form a nested, spatial hierarchy of local, state, and federal land owners. Each level has been granted specific freedoms and responsibilities for land-use decision making by the U.S. Constitution, case law, and statute (Caldwell and Shrader-Fechette 1993) (Table 2 and Fig. 5). Because most of the authority for land-use decisions is vested at the lower levels of this hierarchy, the aggregate effect of land-use change results from many individual decisions that are diffuse in time and space. Authority for planning and zoning rests on three legal traditions of the role of government in (1) reducing harm and nuisances, (2) ensuring orderly timing of development and associated services, and (3) protecting public values (see Callies 1994). However, this process does not recognize the key role of ecological

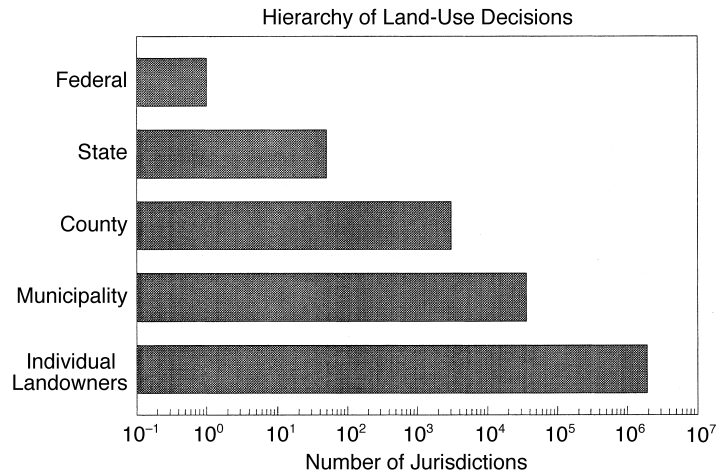
systems in maintaining adequate economic and health conditions.

Private lands

The concept of private ownership of land is one of the most important structural attributes of society in the United States. Private ownership conveys a great deal of leeway to the owner in land-use decisions; yet private land-use decisions also depend on the public provision of infrastructure, environmental quality, and public safety (Smith 1993). Constraints on land use are imposed by government to assure that these needs are met, as well as to deal with "externalities" (Platt 1996). Externalities are current or future effects of land uses that extend beyond the boundaries of individual ownership and thus have the potential to affect surrounding owners. Externalities can be physical (e.g., air or water pollution), biological (e.g., habitat fragmentation), aesthetic (e.g., noise and effects on view sheds), or economic (e.g., changes in commercial activity). The fundamental role of government in land-use decision making is to encourage externalities that enhance the welfare of society and to discourage those that harm it (Smith 1993, Platt 1996).

In playing this role, the government can require land uses on private land to meet standards for public health,

FIG. 5. Hierarchy of domains of influence of decision makers who regulated land use in the United States during 1992. Most authority for land-use choices is vested in the lower levels of the hierarchy: individual landowners and local governments. In this figure, the number of landowners is the number of individual farms in the United States. Data are from the U.S. Bureau of the Census and the U.S. Census of Agriculture (U.S. Department of Commerce, 1975, 1977, 1991, 1996). Note logarithmic scale.



safety, and general welfare (including aesthetics, population density, and environmental quality; Cullingworth 1997). The Constitution confers power on the states to set such standards; the states, in turn, delegate most of that authority to local governments, which control private land use with zoning regulations (Cullingworth 1997). Zoning is a regulatory power that specifies land uses within specific geographic zones (Platt 1996). In short, zoning is a process "... by which the residents of a local community examine what people propose to do with their land and decide whether or not they will permit it" (Garner and Callies 1972: 305).

Furthermore, private land use is indirectly influenced by an array of government policies on everything from taxes to transportation, sometimes with unintended consequences. For example, the tax deduction for home mortgage interest payments, in concert with federal and state highway development, fueled suburbanization and aided the emerging pattern of exurban development in previously rural areas (Kunstler 1993). Current estate and capital-gains tax laws also encourage suburban sprawl and large-lot rural residential development in two ways: (1) Homeowners moving from one housing market to another are encouraged by tax laws to re-invest their appreciated housing investment in a new and often larger home. (2) Estate taxes discourage the passing on of agricultural land from one generation to the next, especially where residential demand has elevated land prices.

Local-government land-use planning

Local land-use planning is effected through "general," "master," or "comprehensive" plans that advise planning and zoning commissions about goals and limits on land use and development. Actual zoning, based on ordinances, requires formal, regulatory action by county commissions or city, town, or village councils

that set permitting criteria for development. Planning attempts to assure that local values are respected and goals for public welfare are met as development proceeds over the long term and over large portions of local jurisdictions. Comprehensive plans are developed with public review and comment, providing a mechanism for citizens' input to and oversight of government influences on land use.

In addition to zoning, local governments have the power to control the subdivision of larger parcels of land, which allows local governments to regulate the spatial distribution of the population within their jurisdiction (Cullingworth 1997). They can set tax rates, which can interact with market forces to determine land-use patterns. Local governments can regulate architectural design, set building codes, and specify standards for sanitation. All of these regulatory actions can constrain the land-use choices of private landowners. However, land-use permitting is an inherently political process in which decision makers are often asked to allow variances from plans.

The state role

In many areas of the United States, state governments have recognized that delegating authority to counties and municipalities can lead to tremendous variation in land-use patterns and in the quality of planning for development. The local focus of land-use authority is particularly problematic in dealing with broad-scale environmental issues like protecting watersheds or endangered species. Jurisdictional fragmentation impedes wise environmental planning (Albrecht et al. 1995).

In response to these problems, many states (notably Florida, New Jersey, Vermont, Oregon, Rhode Island, Georgia, Maine, and Colorado) developed "growth-management" systems that provide a means for state or regional participation in the major decisions that

affect the use of land (Bossleman and Callies 1972, DeGrove 1992, Gale 1992). For example, the Oregon Land Use Act passed in 1973 requires communities and counties to submit plans that must meet state approval. A more recent example is the "Smart Growth Initiative" enacted by Maryland in April 1997. The central component of the Maryland effort is the "Priority Funding Areas" legislation, in which the state works with local governments to use agreed-upon criteria in designating "smart growth areas." Any new development outside of these areas is not eligible for state funding for infrastructure projects. In addition, states can set tax rates to favor particular land uses (for example, agricultural assessments are often lower than residential). States can also purchase land to meet a variety of conservation goals (Platt 1996, Cullingworth 1997).

The federal role

The federal government has little direct role in local land-use planning on nonfederal lands. The Coastal Zone Management Act is one of the very few laws providing for direct federal influence in local land-use planning, either through financial support for planning or as the basis for state legislation. Nevertheless, the federal government can provide strong incentives for particular land uses (e.g., via the Conservation Reserve Program and crop subsidies). Although virtually every decision made by the federal government has some land-use implications (e.g., Cullingworth 1997), some policies are particularly influential, notably housing, transportation, and telecommunications, because these policies provide the means and infrastructure that are required for development.

In contrast with its weak role in private land use, federal agencies have nearly absolute authority over federal lands through laws like the National Forest Management Act and the Federal Land Policy and Management Act, regulating the use of Forest Service and Bureau of Land Management lands. However, indirect effects on management of federal lands also occur through other regulations, such as the National Environmental Policy Act and the Endangered Species Act.

Federal land-use decision making is structured, by legislation, into a much more centralized planning model that, in theory, allows federal agencies to conduct long-term, broad-area, comprehensive planning (see Wilkinson and Anderson 1987, Loomis 1996). The National Forest Management Act (1976) and the Federal Lands Policy and Management Act (1976) mandate comprehensive, long-term, multi-resource, and interdisciplinary planning for the USDA Forest Service and the Bureau of Land Management (the agencies with the largest federal land holdings), respectively. In theory, the land-use "prescriptions" emanating from these

planning processes assign to every parcel of land the "best" mix of uses, including wilderness areas, recreation, logging, and grazing. Environmental criticisms of the first two decades of comprehensive planning for federal lands have led the agencies to modify their strict planning approach to try to incorporate ecosystem-management ideas, including cross-boundary and cross-agency coordination, planning based on ecological considerations as well as on resource outputs, and land-use prescriptions that result in ecologically desirable landscape outcomes (see Christensen et al. 1996). Thus, planning done for federal lands offers a structure that, at least in theory, is more conducive to broad-scale ecological approaches than is private land-use planning in the United States.

ECOLOGICAL PRINCIPLES AND THEIR IMPLICATIONS FOR LAND USE

Changes in technology and modes of production have fundamentally altered the relationship between people and natural ecosystems. When people were sustained by hunting and gathering, the availability and distribution of plant and animal foods limited human population abundance and distribution; hunter-gatherers were tightly integrated into natural food webs. The dependence of humans on natural stocks of plants and animals declined with the advent of agriculture, which allowed people to concentrate in areas with high productivity, areas where soils were fertile and rainfall was abundant. No longer was the spatial distribution of people limited by the availability of "prey." Augmentation of rainfall with irrigation, and addition of fertilizers to natural stocks of nutrients, further reduced the spatial dependence of human population centers on the biotic and abiotic properties of ecosystems. The advent of extensive transportation networks and the development of food-preservation technologies during the Industrial Revolution extended the habitable area by allowing population of areas remote from agriculture.

These trends have reduced the interdependence of ecological and human systems, and the consequences of land-use decisions often are not felt immediately. Planning is needed to avert long-term or broad-scale harmful ecological effects resulting from unwise land-use choices. Therefore, planning should be based upon a sound ecological basis.

The major lessons of ecological science for land management can be summarized in numerous ways. This report organizes ecological information into five principles that have implications for land management. The principles deal with *time*, *place*, *species*, *disturbance*, and the *landscape*. The principles are presented as separate entities, although they interact in many ways. They are translated into specific guidelines in a later section.

Time principle

Ecological processes function at many time scales, some long, some short; and ecosystems change through time. Metabolic processes occur on the scale of seconds to minutes, decomposition occurs over hours to decades, and soil formation occurs at the scale of decades to centuries. Additionally, ecosystems characteristically change from season to season and year to year in response to variations in weather as well as showing long-term successional changes (Odum 1969). Early successional communities often are dominated by a few short-lived and relatively small individuals that grow rapidly and decompose readily after death. In contrast, later successional communities tend to be dominated by a mixture of longer-living species and contain higher standing crops of vegetation that both grow and decompose more slowly. Human activities that alter community composition or biogeochemical cycles can change the pace or direction of ecosystem succession and thus have effects lasting decades to centuries.

The time principle has several important implications for land use. First, the current composition, structure, and function of an ecological system are, in part, a consequence of historical events or conditions that occurred decades to centuries before. An ecosystem may have species or soil characteristics that reflect legacies from past land use (Foster 1992, Motzkin et al. 1996). Therefore, historical information may be needed to understand the nature of the ecosystem, including its responses to changes in use or other perturbations, and current land uses may limit those choices that are available in the future.

Second, the full ecological effects of human activities often are not seen for many years because of the time it takes for a given action to propagate through components of the system. For example, changes in nutrient inputs may alter plant growth rates and species composition (Inouye and Tilman 1995), but these changes in a plant community also affect higher trophic levels, nutrient pools, and soil organic matter, and these latter effects can develop much more slowly.

Third, the imprint of land use may persist on the landscape for a long time, constraining future land use for decades or centuries. For example, the pattern imposed on a forested landscape by extensive clear-cutting may persist for many decades after all harvesting stops (Wallin et al. 1994). Establishing roads and controlling fire or flood regimes have similarly long-lasting effects. Rapid return to previous ecological conditions often does not occur and should not be expected.

Finally, both the variation and the change that characterize ecosystem structure and process mean that the long-term effects of land use or management may be difficult to predict. This problem is exacerbated by the

Box 2. Time—Legacy of Past Land Use on Ecosystem Development

Past land use can constrain or control future ecosystem development, necessitating long-range planning of land use. For example, Foster (1992) and Motzkin et al. (1996) show that the current composition of forests in parts of New England is a result of past patterns and practices in agriculture and forestry. During the 18th and 19th centuries most of the forests in New England were either cleared for agriculture or harvested for wood products. By the late 19th century, agricultural lands were neglected, and forest vegetation was reestablished. By the mid-1900s, forest cover was practically back to presettlement levels. However, current forest composition shows the imprint of past land use.

In a sand plain in Massachusetts, forests of pitch pine (*Pinus sylvestris*) occur almost exclusively on formerly plowed lands; in contrast, stands of scrub oak occur mostly on sites that had not been plowed (Motzkin et al. 1996). The soils from these two vegetation types looked different because of the 20-cm-deep plow layer under the pitch pine forest; however, chemical and physical analysis of the soils suggested that the plowing caused only minor alterations because of the short duration and low intensity of agriculture on this marginal sandy site. Nevertheless, the effects of this low-intensity past land use on current vegetation are striking.

Paleoecological evidence suggests that pre-European fires were common on New England sand plains. The impacts of fire and prior land use on vegetation interact. Fire thus influences vegetation patterns in the sand plain of New England and can explain some of the dramatic changes in land cover that have occurred (Motzkin et al. 1996). For example, pitch pine requires the exposed mineral soil and open canopy conditions that exist on formerly plowed sites when frequent fires are absent. Motzkin et al. (1996) conclude that the modern vegetation on the sand plain is a result of complex anthropogenic disturbance histories, with fire modifying the composition of species assemblages that developed as a result of prior land use.

tendency to overlook low-frequency ecological disturbances, such as 100-yr flooding or storm events (Dale et al. 1998) or processes that operate over periods longer than human life spans (e.g., forest succession).

Species principle

Particular species and networks of interacting species have key, broad-scale ecosystem-level effects. These focal species affect ecological systems in diverse ways. *Indicator species* are important because their condition is indicative of the status of a larger functional group of species, reflective of the status of key habitats, or symptomatic of the action of a stressor. *Keystone species* have greater effects on ecological processes than would be predicted from their abundance or biomass alone (Power et al. 1996). *Ecological engineers* [e.g., the gopher tortoise (*Gopherus polyphemus*) or beaver (*Castor canadensis*)] alter the habitat and, in doing so, modify the fates and opportunities of other species (Jones et al. 1994, Naiman and Rogers 1997). *Umbrella species* either have large area requirements or use multiple habitats and thus overlap the habitat requirements of many other species. *Link species* exert critical roles in the transfer of matter and energy across trophic levels or provide critical links for energy transfer within complex food webs. Trophic cascades occur when changes in the abundance of a focal species or guild of organisms at one trophic level propagate across other trophic levels, resulting in dramatic changes in biological diversity, community composition, or total productivity. Such cascades often affect many species, including those with which the guild does not interact directly (Power 1992, Polis and Wine-miller 1996). For instance, changes in the abundance of top predatory fishes may change phytoplankton composition and alter the productivity of a lake (Carpenter and Kitchell 1988, Carpenter 1992). In addition, some species (such as threatened and endangered species, game species, sensitive species, and those that are vulnerable to society because of their rarity) also require attention because of public interest in them.

The impacts of changes in the abundance and distribution of focal species are diverse. For example, keystone species affect ecosystems through such processes as competition, mutualism, dispersal, pollination, and disease and by modifying habitats and abiotic factors. Because the effects of keystones are diverse and involve multiple steps, they are often unexpected despite their fundamental importance to biological diversity and ecosystem dynamics (Paine 1969, Paine 1995, Power et al. 1996). The removal of a keystone species can radically change the diversity and trophic dynamics of a system. Changes in land use that affect keystone species may spread well beyond the boundaries of a land-use unit, extending land covers that are inhospitable to some species and favorable to others, adding barriers to movement or dispersal, introducing new predators or competitors, or changing the existing trophic or competitive dynamics. While keystone species

have been found in many ecosystems, they are difficult to identify, and their effects are difficult to predict prior to a change in their abundance (Power et al. 1996). Often it is the processes associated with particular species that are critical to ecosystem functions.

A nonnative species can assume a focal-species role when introduced into an ecosystem and produce numerous effects on the ecosystems. Nonnative species have altered community composition and ecosystem processes via their roles as predators, competitors, pathogens, or vectors of disease and through effects on water balance, productivity, and habitat structure (Drake et al. 1989). However, determining whether a particular nonnative species will become a focal species when introduced to a new ecosystem is very difficult (Drake et al. 1989). Changes in land use often affect the establishment of nonnative species. For example, both agriculture and grazing typically are based upon nonnative species. In these situations, the nonnative species often are used at very high densities and can significantly alter environmental conditions, thereby reducing the abundance of native species and creating conditions under which introduced species can spread. Furthermore, changes in the *pattern* of land cover can promote the establishment of nonnative species, for example by creating corridors of disturbed habitat that alter movement patterns (Getz et al. 1978, DeFerrari and Naiman 1994).

Changes in species composition and diversity can result from land use through alterations to such ecosystem properties as stream turbidity (which often occurs with increased soil erosion), nutrient cycling, or productivity (e.g., Rosenzweig and Abramsky 1993). Additions of water or fertilizer also typically alter and often reduce biodiversity (Harms et al. 1987, Warner 1994, Naiman et al. 1995). The effects of land use on species composition have implications for the future productivity of ecological systems. Low-diversity systems are likely to experience large variations in realized productivity through time, as species differ in their productive potential under different conditions of weather or resource supply (Mitchell 1984, McNaughton 1993, Rosenzweig and Abramsky 1993, Tilman 1996). Moreover, land uses that result in low species diversity can cause resources to be used less fully than they might be in a more ecologically diverse community of primary producers (Ewel et al. 1991). However, some land uses do not affect diversity of native or introduced species and have little impact on ecosystem processes (e.g., grazing; Stohlgren et al. 1999). Nevertheless, herbivores can affect the productivity of the plant communities they graze (McNaughton 1979, 1993), and top predators can initiate trophic cascades that influence productivity by changing the primary-producer community (Carpenter 1992). In fact, the in-

Box 3. Species Linkages Among Species

Pollinators, woodpeckers, and salt cedar each illustrate critical features of linkages between species. Insect pollinators are a keystone group of species because more than two thirds of flowering plants require them for successful reproduction (Tepedino 1979). A reduction in pollinators can lead to reduced seed set and less viable progeny, subsequently affecting other species that feed on plant seeds or fruits (Kearns and Inouye 1997). Changes in land use and management have negatively affected plant pollinators in many places. In both North America and Europe, pollinator density is inversely related to the proportion of an area occupied by agriculture, presumably because conversion of land to agriculture or urban areas reduces the amount of native food plants used by pollinators. Similarly, habitat fragmentation and pesticide use can reduce or eliminate pollinator populations (Johansen 1977, Jennersten 1988, Lamont et al. 1993). For example, the populations of several species of native bees declined sharply after forests in New Brunswick, Canada, were sprayed with insecticide to control spruce budworm (*Choristoneura fumiferana*). Subsequently, several species of understory plants that rely on insect pollination had reduced fecundity (Thomson et al. 1985).

The Red-cockaded Woodpecker (*Picooides borealis*) is an example of a keystone species that affects the habitats of other organisms. It lives in the longleaf pine–wire grass ecosystem of the southeastern United States, which has declined by >98% between 1880 (presettlement) and 1986 (Noss and Peters 1995). These birds nest in mature longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pine trees and are the only species in this ecosystem that excavate nest cavities in living trees (Rudolph and Conner 1991). Red-cockaded Woodpeckers are key components of this system because numerous other species of birds, mammals, reptiles, amphibians, and insects rely on the nest cavities excavated by the woodpeckers (Dennis 1971). These other animals have been reduced in abundance over the past century because populations of the woodpecker have declined as mature pine-forest habitat has been reduced by timber harvest and conversion to agriculture (Conner and Rudolph 1991).

Finally, introduced species may affect the composition and structure of systems in which they become established. Following the conversion of land to agriculture in the late 19th century, salt cedar (*Tamarisk chinensis*) was introduced into the western United States to provide windbreaks and to prevent soil loss (Walker and Smith 1997). Salt cedar invaded water drainages, riparian ecosystems, and wetland habitat over much of western North America. The dominance of salt cedar in such habitats results in reduced plant and animal diversity; increased evapotranspiration; a lower water table; increased soil salinity; and, possibly, altered nutrient cycling (Hunter et al. 1988, Busch and Smith 1995, Walker and Smith 1997).

roduction of predators has been used as a remediation tool to control agricultural pests and undesired algae in lakes.

Place principle

Local climatic, hydrologic, edaphic, and geomorphologic factors as well as biotic interactions strongly affect ecological processes and the abundance and distribution of species at any one place. Local environmental conditions reflect location along gradients of elevation, longitude, and latitude and the multitude of microscale physical, chemical, and edaphic factors that vary within these gradients. These factors constrain the locations of agriculture, forestry, and other land uses, as well as provide the ecosystem with a particular appearance. A Great Basin site looks different and has a different landscape structure from that of the Sonoran Desert, an arid montane grassland, an eastern deciduous forest, or the Great Plains. Moreover,

local environmental conditions constrain the patterns of land use.

Alternatively, the constraints of place provide opportunities to use ecological patterns and processes as models for efficient and sustainable land use. Rates of key ecosystem processes, such as primary production and decomposition, are limited by soil nutrients, temperature, water availability, and the temporal pattern of availability of these factors as mediated by climate and weather (Chabot and Mooney 1985, Givnish 1986, Frank and Inouye 1994). Thus, only certain ranges of ecological-process rates can persist in a locale without continued management inputs (e.g., irrigation of crops growing in a desert). Chronic human intervention may broaden these ranges but cannot entirely evade the constraints of place. For instance, enhanced productivity on desert uplands can be supported over the short term by additions of water; however, higher productivity generally cannot be sustained in arid-land soils over

Box 4. Place—Using Land Within the Constraints of Place: Agricultural Ecology

Ethnobotanist Gary Nabhan (1982, 1986) reports many cases of indigenous agricultural systems that illustrate the value of using naturally occurring ecosystems as models for sustainable agriculture. For centuries, native peoples of the desert southwestern United States sustained agricultural production by using both wild desert plants and domesticated relatives of desert-adapted plants, even though these areas are only marginally arable because of limited water and soil nutrients. They cultivated such wild desert plants as amaranth and agaves and domesticated varieties of panic grass, legumes, and desert squashes, many of which were grown in mixed-crop fields. These plants are adapted to the low and variable rainfall, relatively nutrient-poor soils, and high and variable temperatures of the local environment. They maintained production under conditions that cause failure of plants not so adapted. These traditional agricultural systems indicate the value of using the landscape in a way consistent with sustainable ecosystem function. Native Americans of the southwest not only used many varieties of desert plants as the basis of their agriculture but also located agricultural areas across the landscape in a way that took advantage of local variation in water availability and soils. For instance, crops were planted on flood plains following the pattern of emergence of desert annual plants after seasonal rainfall. These areas of the landscape received regular inputs of silt as well as water, and the phenology of the native annuals provided cues to the best times for agricultural planting and production. The interspersed patches of agriculture with natural vegetation also increased access to a reliable pool of pollinators and to soil mutualists, such as bacteria and mycorrhizal fungi, that were adapted to local soils and plants.

the long run because of the degrading effects of high evapotranspiration rates and resulting salinization.

Agricultural production requires favorable conditions of temperature, soil, nutrients, and water—key limiting factors for plant growth and productivity. The temporal pattern of these factors is a consequence of climate and weather, restricting the location of agriculture and the suitability of particular crops. Using plants appropriate for a particular place and situating agricultural and natural patches of vegetation in an ap-

propriate landscape context can allow sustainable agricultural land use, reduce the impacts of agriculture on adjacent areas, and permit more efficient use of resources. Many uses of land have failed because species composition and ecosystem processes have not been appropriately matched with the local physical, chemical, and climatic conditions. For example, the Dust Bowl in the central United States resulted from unsustainable use of Great Plains arid grassland for dryland row-crop agriculture (Sears 1980, Glantz 1994, Diamond 1997). In addition, agricultural land uses can influence regional climate, vegetation, and stream flow patterns (Stohlgren et al. 1998).

Naturally occurring patterns of ecosystem structure and function provide models for sustainable and ecologically sound agriculture (Carroll et al. 1990, Soulé and Piper 1992). Only those species whose adaptations suit the environmental constraints particular to an area will thrive there. For instance, arid regions cannot support plants that are unable to survive high heat and low water availability. Precipitation constrains choice of species for landscape plantings as well as for managed agricultural, forestry, or grazing systems. It also makes some places more important than others for conservation of species and ecosystems. Species lost as a consequence of land-cover changes or with increases in land-use intensity may not be easily restored or replaced. Agricultural plants may be selected to mimic the structure, physiology, growth, and flowering/fruiting phenology of local communities as a mechanism to match productive potential with local patterns of conditions suitable for production. Similarly, the use of multiple crops, typical of traditional low-technology agriculture, has attracted recent attention as a way of increasing the efficiency of resource use, stabilizing production across years of varying weather conditions, and reducing the impact of herbivores.

Land uses that cannot be maintained within the constraints of place will be costly when viewed from long-term and broad-scale perspectives. Only certain patterns of land use, settlement and development, building construction, or landscape design are compatible with local and regional hydrology and geomorphic conditions, as well as biogeochemical cycles. In terrestrial systems, land-use and land-management practices that lead to soil loss or degradation reduce the long-term potential productivity of a site and can affect species composition. Land-use practices can also influence local climate (e.g., as expressed by the urban heat-island concept). Additions of water and nutrients may exceed levels that can be used directly by primary producers, given the natural limitations of species and climate. The excess water and nutrients from enriched systems may move into adjacent areas and influence ecosystems by such processes as runoff. Similarly, sustainable set-

tlement is limited to suitable places on the landscape. For instance, houses or communities built on transient lakeshore dunes, major flood plains, eroding seashores, or sites prone to fires are highly vulnerable to loss over the long term. Ideally, the land should be used for the purpose to which it is best suited. It does not make sense to put cities on prime farmland, requiring that more moderately productive farmland be used to provide the same quantity of food production. However, socioeconomic and political pressures have strong influences over land-use decisions.

Disturbance principle

The type, intensity, and duration of disturbance shape the characteristics of populations, communities, and ecosystems. Disturbances are events that disrupt ecological systems. Disturbances may occur naturally (e.g., wildfires, Romme and Despain 1989; storms, Boose et al. 1994, Lugo and Scatena 1996; or floods, Poff et al. 1997) or be induced by human actions, such as clearing for agriculture, clear-cutting in forests, building roads, or altering stream channels. The effects of disturbances are controlled in large part by their intensity, duration, frequency, timing, and spatial impacts (the size and shape of the area affected) (Sousa 1984, Pickett and White 1985, Pickett et al. 1987a, Reice 1994, Turner et al. 1997a). Disturbances may affect both above- and belowground processes (e.g., soil carbon pools and nutrient cycling). Disturbance has been shown to have many important effects on communities and ecosystems, including enhancing or limiting biological diversity (Hastings 1980, Sousa 1984); initiating succession (Cowles 1911, Watt 1947, Pickett et al. 1987a, b, Glenn-Lewin and van der Maarel 1992); causing inputs or losses of dead organic matter and nutrients that affect productivity and habitat structure (Peet 1992, Scatena et al. 1996); and creating landscape patterns that influence many ecological factors, from movements and densities of organisms to functional attributes of ecosystems (Turner 1987, Turner et al. 1994, 1997b, Forman 1995). Disturbance and succession impose both spatial and temporal heterogeneity on ecological systems. Additionally, disturbances can have secondary effects, such as fragmentation caused by road development, plowing, or clear-cutting (Franklin and Forman 1987, Roland 1993).

Land-use changes that alter natural-disturbance regimes or initiate new disturbances are likely to cause changes in species' abundance and distribution, community composition, and ecosystem function (Yarie et al. 1998). In addition, the susceptibility of an ecosystem to other disturbances may be altered. For example, forest fragmentation may enhance the susceptibility of the remaining forest to a variety of other disturbances, including windthrow, pest epidemics, invasion by non-

native species, and nest parasitism (Franklin and Forman 1987).

Land managers and planners should be aware of the ubiquity of disturbance in nature. Disturbances that are both intense and infrequent, such as hurricanes or 100-yr floods, will continue to produce "surprises" (Turner et al. 1997a, Turner and Dale 1998). As discussed above for the time principle, communities and ecosystems change, with or without disturbance; thus, attempts to maintain landscape conditions in a particular state will be futile over the long term. Further, attempts to control disturbances are generally ineffectual (Dale et al. 1998). In fact, suppression of a natural disturbance may have the opposite effect of that intended. For example, suppression of fire in fire-adapted systems results in the buildup of fuels and increases the likelihood of severe, uncontrollable fires. In the aftermath of the fires at Yellowstone National Park, it was recognized that the large scale of those fires was, in part, the result of previous fire-control actions that created connected patches of fire-prone forests (Schullery 1989). Similarly, flood-control efforts have facilitated development in areas that are still subject to infrequent large events (e.g., the 1993 floods in the upper Midwest), resulting in tremendous economic and ecological loss (Sparks 1996, Haeuber and Michener 1998, Sparks et al. 1998). Land-use policy that is based on the understanding that ecosystems are dynamic in both time and space can often deal with changes induced by disturbances (Turner et al. 1995, Dale et al. 1998, Haeuber and Michener 1998).

Natural disturbances can provide a model upon which to base land-use activities, but the differences between natural and human activities must be recognized. For example, timber harvest has sometimes been considered a surrogate for natural fire, but some of the ecological attributes and effects of these two disturbances are markedly different. Natural forest fire typically causes little soil disturbance; and often fine fuels are consumed, while large, coarse wood remains to decompose after the fire. Timber harvest often results in considerable soil disturbance, and fine branches may remain while large wood is removed. This removal of wood also impacts forest streams, which are strongly influenced by the physical structure and nutrient subsidies provided by dead woody debris (Harmon et al. 1986, Bilby and Bisson 1998).

Continued expansion of human settlement into disturbance-prone landscapes is likely to result in increased conflicts between human values and the maintenance of natural-disturbance regimes necessary to sustain such landscapes. For example, building homes in conifer forests that have recurrent wildfires results in conflicts that endanger human life as well as entail financial risks.

Box 5. Effects of Altered Disturbance Regimes

Episodic disturbance shapes the structure and function of ecosystems by changing the composition of communities (Milchunas and Lauenroth 1995, Tabacchi et al. 1996, Tanner et al. 1996), altering linkages in food webs (Tanner et al. 1994, Warren and Spencer 1996, Wootton et al. 1996), modifying fluxes of nutrients (Hobbs and Schimel 1984, Rowcliffe et al. 1995, Belknap and Naiman 1998), and altering the basic physical structure of ecosystems (Turner et al. 1997a, b). Shifts in land use can cause profound changes in disturbance regimes and, in so doing, can drive fundamental changes in ecosystems remote from those where the original land-use change occurred.

An example of such change is seen in riparian communities along the headwaters of the North Platte River in Wyoming and Nebraska (Knopf and Scott 1990, Miller et al. 1995). During the second half of the 19th century and continuing into the 20th century, large areas of prairie grasslands in the western United States were converted to cropland (Knopf and Sampson 1994). In Nebraska, almost 12 000 km² of mixed and tallgrass prairie, used primarily for grazing, were converted to other uses, mostly intensive agriculture. Because the region is arid, this conversion required irrigation, creating widespread demands for stored water that could be periodically released to augment rainfall. Demands for irrigation were exacerbated by urbanization and the need for predictable water supplies for growing cities. By 1915 the entire summer flow of the North Platte was committed to agricultural, residential, and industrial users (Knopf and Scott 1990).

In response to these demands, the region witnessed extensive impoundment of water to store runoff. Cumulative storage of water in the northern basins increased from 0 to almost 9000 km³ between 1885 and 1980 (Eschner et al. 1983, Knopf and Scott 1990). In addition, elaborate canal systems were constructed to irrigate river terraces (Eschner et al. 1983). The construction of reservoirs and canals caused profound changes in the flood regimes of the North Platte. Maximum flow rates were reduced to 20% of historic levels, while mean discharge rates were decreased 85% (Knopf and Scott 1990).

Changes in hydrology caused widespread change in the morphology of the river and in the composition of the biotic communities surrounding it (Knopf and Scott 1990). Historically, the Platte headwaters were subject to annual floods, creating a broad, braided floodplain. These annual floods prevented the establishment of woody vegetation, which occurred primarily as scattered stands of cottonwood (*Populus sargentii*) and willow (*Salix* spp.). Woody vegetation was limited to areas where groundwater was near the rooting zone, seedlings were not submerged for long periods during runoff, and seedlings were sheltered from the scouring effect of floods (Knopf and Scott 1990). Reduction in peak flows increased habitat suitable for woody plants by reducing the scouring effect of spring floods and by shrinking areas that were submerged. However, some habitats were made less favorable for riparian species as a result of changes in the distribution of groundwater near the soil surface. As a result, a variety of successional woody species, including eastern red cedar (*Juniperus virginiana*), Russian olive, (*Elaeagnus angustifolia*), and green ash (*Fraxinus pennsylvanica*), encroached onto formerly active river channels (Knopf 1986, Knopf and Scott 1990) while recruitment of cottonwoods declined in some areas (Miller et al. 1995). These trends led to marked shifts in the composition of plant and animal communities (Knopf 1986, Knopf and Scott 1990) and in the structure of landscapes surrounding the river (Miller et al. 1995).

Landscape principle

The size, shape, and spatial relationships of land-cover types influence the dynamics of populations, communities, and ecosystems. The spatial array of habitats or ecosystems comprises the landscape, and all ecological processes respond, at least in part, to this landscape template (Urban et al. 1987, Turner 1989, Forman 1995, Pickett and Cadenasso 1995). The kinds of organisms that can exist (including their movement patterns, interactions, and influence over such ecosystem processes as decomposition and nutrient fluxes)

are constrained by the sizes, shapes, and patterns of interspersion of habitat across a landscape. Large decreases in the size of habitat patches or increases in the distance between habitat patches of the same type can greatly reduce or eliminate populations of organisms (Lovejoy et al. 1986, Saunders et al. 1991, Noss and Csuti 1994, Hansson et al. 1995, Fahrig 1997, Schwartz 1997) as well as alter ecosystem processes.

Human-settlement patterns and individual land-use decisions often fragment the landscape or otherwise alter land-cover patterns. Effects of habitat fragmen-

Box 6. Landscape—Wolves in a Human-Dominated Landscape

The status and future of wide-ranging animals in regions increasingly dominated by humans is often a concern to ecologists and natural-resource managers, especially because management must be considered at large spatial scales and not be limited to small reserves. Recovery of the gray wolf (*Canis lupus*), listed in 1973 as an endangered species, illustrates this challenge. The wolf was extirpated throughout most of the conterminous United States following European settlement, with remnant populations persisting only in northeast Minnesota and on Isle Royale, Michigan. Natural recolonization in the western Great Lakes region since the 1970s has led to recovery of wolf populations, and the Wisconsin and Michigan populations each number between 80 and 90 animals (Mladenoff et al. 1997). Wolf recovery resulted largely from legal protection and changed public attitudes in which the existence of wolves is tolerated (Mech et al. 1995). In addition, large populations of deer (*Odocoileus virginianus*) that have resulted, in part, from the fragmented forest landscapes typical of the region today, provide a ready source of prey. But how does the current landscape configuration in this human-dominated region influence the wolf habitat and populations?

A regional analysis of wolf colonization in the western Great Lakes region from 1979 to 1993 revealed a number of landscape-scale characteristics important for wolf habitat use (Mladenoff et al. 1995). Wolves avoided certain land-cover classes, such as agriculture and deciduous forests, and favored forests with at least some conifers. Public lands received more use, and private lands were avoided. Wolf packs were also most likely to occur in areas with road densities below 0.23 km/km², and nearly all wolves occurred where road densities were <0.45 km/km². No wolf-pack territory was bisected by a major highway (Mladenoff et al. 1995). Rapid increases in the wolf population since 1993 have occurred in northern Michigan, where favorable habitat is more abundant and more highly connected than in Wisconsin (Mladenoff et al. 1997). In Wisconsin, favorable wolf habitat occurs in relatively small, isolated areas separated by lands with greater road density and human development. Adult wolf mortality in Wisconsin has been high, with dispersing wolves being most vulnerable as they cross lands with more intensive human use. Thus, current landscape configurations suggest that wolf-population increases will be more rapid in northern Michigan than in Wisconsin. Colonization of the fragmented habitat in Wisconsin may remain dependent on dispersers arriving from larger, saturated populations in Minnesota.

tation on species are numerous (e.g., Saunders et al. 1991, Noss and Csuti 1994, Andren 1997). Landscape fragmentation is not necessarily destructive of ecological function or of diverse biological communities, because a patchwork of habitat types often maintains more types of organisms and more diversity of ecosystem process than does a large area of homogeneous habitat (e.g., Wilson et al. 1997). Making a naturally patchy landscape less patchy (more uniform) may also have adverse effects.

Larger patches of habitat generally contain more species (and often a greater number of individuals) than smaller patches of the same habitat (Wiens 1996). Larger patches also frequently contain more local environmental variability, such as differences in microclimate, more structural variation in plants, and greater diversity of topographic positions. This variability provides more opportunities for organisms with different requirements and tolerances to find suitable sites within the patch. In addition, the edges and interiors of patches may have quite different conditions, favoring some species over others, and the abundance of edge and interior habitat varies with patch size (Temple 1986). Large

patches are likely to contain both edge and interior species, whereas small patches will contain only edge species.

Habitat connectivity can constrain the spatial distribution of species by making some areas accessible and others inaccessible (Burgess and Sharpe 1981, Pulliam et al. 1992). Connectivity is a threshold dynamic, meaning that gradual reduction of habitat may have gradual effects on the presence or abundance of a species, but the effects tend to be dramatic after the threshold is passed (Andren 1997). Land-cover changes are most likely to have substantial effects when habitat is low to intermediate in abundance (Pearson et al. 1996). Under these conditions, small changes in habitat abundance may cause the connectivity threshold to be passed. The threshold of connectivity varies among species and depends on two factors: (1) the abundance and spatial arrangement of the habitat and (2) the movement or dispersal capabilities of the organism (Gardner et al. 1989, Pearson et al. 1996).

Local ecological dynamics (e.g., the abundance of organisms at a place) may be explained by attributes of the surrounding landscape as well as by character-

istics of the immediate locale (e.g., Franklin 1993, Pearson 1993). Valone and Brown (1995) found that rates of immigration and extinction of small rodents in habitat patches were affected by competition from other species and by habitat structure. Therefore, understanding the implications of local land-use decisions requires interpreting them within the context of the surrounding landscape.

The ecological import of a habitat patch may be much greater than is suggested by its spatial extent. Some habitats, such as bodies of water or riparian corridors, are small and discontinuous, but nevertheless have ecological impacts that greatly exceed their spatial extent (Naiman and Décamps 1997). For example, wetlands and bodies of water in general are low in spatial extent but high in their contributions to the compositional and structural complexity of a region. In addition, the presence of riparian vegetation, which may occur as relatively narrow bands along a stream or as small patches of wetland, generally reduces the amount of nutrients being transported to the stream (e.g., Peterjohn and Correll 1984, Charbonneau and Kondolf 1993, Detenbeck et al. 1993, Soranno et al. 1996, Weller et al. 1998). This filtering by the vegetation is an ecologically important function because excess nutrients that unintentionally end up in lakes, streams, and coastal waters are a major cause of eutrophication. Thus, the presence and location of particular vegetation types can strongly affect the movement of materials across the landscape and can contribute to the maintenance of desirable water quality.

GUIDELINES FOR LAND USE

Ecologically based guidelines are proposed here as a way to facilitate land managers considering the ecological ramifications of land-use decisions. These guidelines are meant to be flexible and to apply to diverse land-use situations. The guidelines recognize that the same parcel of land can be used to accomplish multiple goals and require that decisions be made within an appropriate spatial and temporal context. For example, the ecological implications of a decision may last for decades or even centuries, long outliving the political effects and impacts. Furthermore, all aspects of a decision need to be considered in setting the time frame and spatial scale for impact analysis. In specific cases, the relevant guidelines can be developed into prescriptions for action. One could think of these guidelines as a checklist of factors to be considered in making a land-use decision:

- 1) Examine the impacts of local decisions in a regional context.
- 2) Plan for long-term change and unexpected events.
- 3) Preserve rare landscape elements, critical habitats, and associated species.

4) Avoid land uses that deplete natural resources over a broad area.

5) Retain large contiguous or connected areas that contain critical habitats.

6) Minimize the introduction and spread of nonnative species.

7) Avoid or compensate for effects of development on ecological processes.

8) Implement land-use and land-management practices that are compatible with the natural potential of the area.

Checking the applicability of each guideline to specific land-use decisions provides a means to translate the ecological principles described in the previous section into practice.

Examine impacts of local decisions in a regional context

As embodied in the landscape principle, the spatial array of habitats and ecosystems shapes local conditions and responses (e.g., Risser 1985, Patterson 1987) and, by the same logic, local changes can have broad-scale impacts over the landscape. Therefore, it is critical to examine both the constraints placed on a location by the regional conditions and the implications of decisions for the larger area. This guideline dictates two considerations for planning land use: identifying the surrounding region that is likely to affect and be affected by the local project and examining how adjoining jurisdictions are using and managing their lands. Once the regional context is identified, regional data should be examined. Items to include in a regional data inventory include land-cover classes, soils, patterns of water movement, historical disturbance regimes, and habitats of focal species and other species of special concern (see Diaz and Apostol [1992] and Sessions et al. [1997] for a thorough discussion). The focal species typically represent a diversity of functional roles that are possible within a place and reflect the environmental fluctuations that provide opportunities and constraints for species. In some cases, an attribute (such as soils) can be used as a surrogate for other information that is dependent on that feature (such as vegetation). Recent technological advances—such as the development of geographic information systems (GIS) and the general availability of databases for soils, roads, and land cover on the Internet—make regional analysis a possibility even for small projects (e.g., Mann et al. 1999).

Where one has the luxury of planning land use and management in a pristine site, both local and broad-scale decisions can be considered simultaneously. Forman (1995) suggests that land-use planning begin with determining nature's arrangement of landscape elements and land cover and then considering models of

Box 7. Assessing local conditions

The purpose of land-use planning is to ensure that important societal attributes are sustained. These attributes fall into three groups: (1) infrastructure (e.g., jobs, roads, schools, and firehouses), (2) environmental resources (e.g., open spaces, parks, watersheds, natural areas, and wetlands), and (3) public safety (e.g., avoidance of flood plains, unstable soils, and fire hazards). Land-use planning typically follows several steps in balancing emphasis on these attributes.

First, data on current local conditions are assembled. On the basis of these data, concerns about impacts of development are identified. Then, goals for maintaining values are formulated, and criteria for meeting those goals are specified. For example, criteria for meeting the goal of preserving vistas might be described in terms of proportions of the skyline visible from a set of locations within the planning area. Alternative approaches to meeting those goals (for example, regulations, incentives, or public purchase) are developed, and the best are selected and implemented. The success of the chosen approach is then evaluated relative to the criteria. This evaluation becomes part of the data used in the next iteration of the planning process.

An important step in land-use planning is trying to ascertain how a proposed use will affect current local conditions. As an illustration, we describe a process for identifying the effects of development on wildlife habitat and natural communities in Larimer County, Colorado. The process was initiated by assembling a group of stakeholders to work with ecologists to identify areas of the landscape that needed to be protected. This group included developers, landowners, planners, environmental advocates, and decision makers. The participation of stakeholders was important for several reasons. First, no single "ecological standard" can be used to assess the value of one facet of the landscape relative to another. Ultimately, ecological knowledge must be combined with local values to arrive at such assessments. Second, the support of leaders of groups affected by the process must be enlisted.

The stakeholder group identified four landscape features based on (1) importance to biological conservation and (2) availability of spatial data about the features (Table 3). These features were mapped, and a composite map was created (Fig. 6). It showed all of the county as falling into one or more of the four categories. This map was used to designate areas that required a "Habitat Mitigation Plan." As a requirement for approval of all proposed developments, these plans outline procedures for on-the-ground verification and assessment of the condition of these environmental features. If the features are determined to be at risk with the proposed land use, then steps must be taken to mitigate the effects of development. Such steps include provision of setbacks, enforcement of special regulations and covenants, and transfer of development rights from other areas.

Developers can specify an area in the County and learn if it contains environmentally sensitive areas *before* preparing a development proposal, increasing the chances that sensitive areas will be avoided by choice rather than by regulation. Alternatively, citizen advocates can learn where development is proposed and can attend review hearings with the support of the best available data on the environmental impacts of the development under review. This mechanism allows the assessment of local conditions to be a dynamic, ongoing process, rather than static and one-time.

TABLE 3. Local features mapped for environmental protection as part of the Partnership Land Use System (PLUS) developed by Larimer County, Colorado, USA.

Environmental value	Definition	Data source
Conservation sites	Areas containing one or more imperiled species (plants or animals)	Field surveys by Colorado Natural Heritage Program
Habitat for economically important species	Winter range and migration corridors for mule deer, elk, and pronghorn antelope	Field surveys by Colorado Division of Wildlife
Areas of high species richness	Areas where predicted vertebrate species richness exceeds 95% of all areas included in the analysis	Vegetation map derived from Thematic Mapper satellite image Habitat modeled from vegetation associations of all vertebrate species in county
Rare plant communities	Plant communities covering <3% (individually) of the land area of the county	Vegetation map derived from Thematic Mapper satellite image

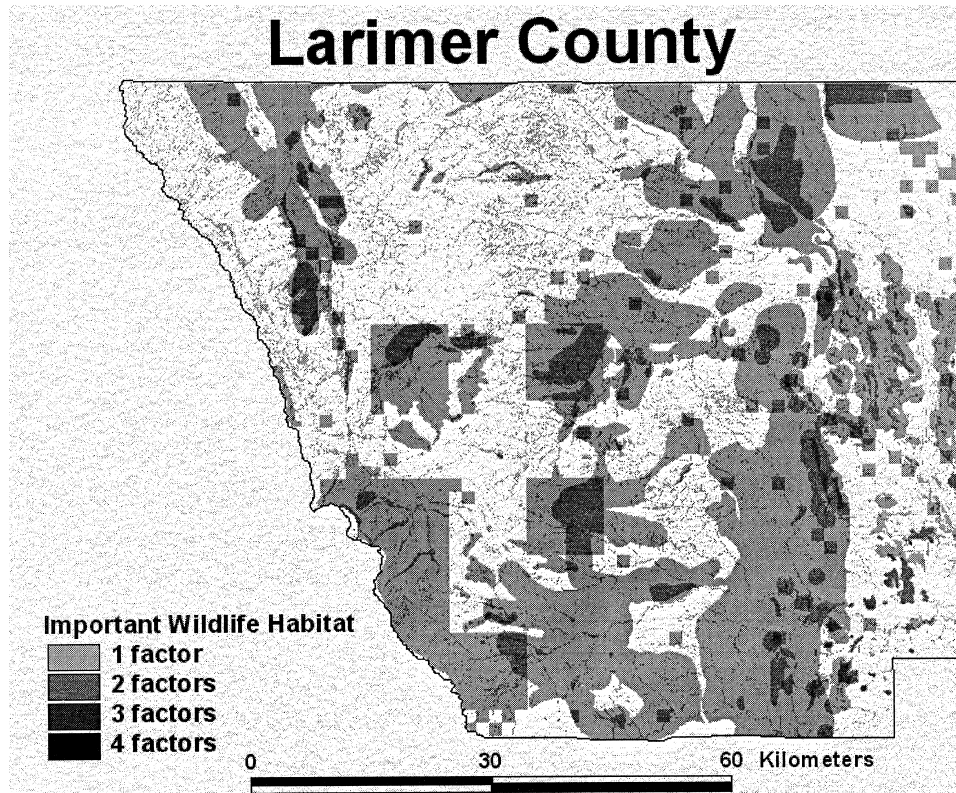


FIG 6. Map of important wildlife habitat in Larimer County, Colorado, USA. Shaded areas show parts of the county containing one or more of the following factors: range vegetation types, high species richness, habitat for economically important vertebrates, and habitat for rare and sensitive plants and animals. See Table 3 for elucidation of factors.

optimal spatial arrangements and existing human uses. Following this initial step, he suggests that the desired landscape mosaic be planned first for water and biodiversity; then for cultivation, grazing, and wood products; then for sewage and other wastes; and finally for homes and industry. Planning under pristine conditions is typically not possible. Rather, the extant state of development of the region generally constrains opportunities for land management.

This guideline implies a hierarchy of flexibility in land uses, and it implicitly recognizes ecological constraints as the primary determinants in this hierarchy. A viable housing site is much more flexible in placement than an agricultural area or a wetland dedicated to improving water quality and sustaining wildlife. Optimizing concurrently for several objectives requires that planners recognize lower site flexibility of some uses than others. However, given that most situations involve existing land uses and built structures, this guideline calls for examining local decisions within the regional context of ecological concerns as well as in relation to the social, economic, and political perspectives that are typically considered.

Ideally, land-use models that incorporate both ecological and other concerns about impacts of land activities could be used to design and explore implications of land-use decisions in a regional context. Land-use models that truly integrate the social, economic, and ecological considerations are in their infancy, and no consensus has yet been reached about what approaches are best for this task. Therefore, many diverse approaches have been advanced (Wilkie and Finn 1988, Southworth et al. 1991, Baker 1992, Lee et al. 1992, Dale et al. 1993, 1994a,b, Riebsame et al. 1994, Gilruth et al. 1995, Turner et al. 1996, Wear et al. 1996). Development and use of these models have improved understanding of the relationship between the many factors that affect land-use decisions and their impacts—including human perceptions, economic systems, market and resource demands, foreign relations (e.g., trade agreements), fluctuations in interest rates, and pressure for environmental conservation and maintenance of ecosystem goods and services. Understanding this interface between causality and effect of land-use decisions is a key challenge facing the scientific community and planners in the coming decades.

Plan for long-term change and unexpected events

The time principle indicates that impacts of land-use decisions can, and often do, vary over time. Long-term changes that occur as a response to land-use decisions can be classified into two categories: delayed and cumulative. Delayed impacts may not be observed for years or decades. An example is the composition of forest communities in New England; today those forests differ substantially among areas that were previously woodlots, pasture, or croplands (Foster 1992) (see Box 2). Cumulative effects are illustrated by events that together determine a unique trajectory of effects that could not be predicted from any one event (Paine et al. 1998). For example, at Walker Branch Watershed in East Tennessee, patterns of calcium cycling are determined not only by past land uses (timber harvest vs. agriculture) but also by the history of insect outbreaks in the recovering forest (Dale et al. 1990).

Future options for land use are constrained by the decisions made today as well as by those made in the past. These constraints are conspicuous in forested systems, where options for areas to harvest may be limited by the pattern of available timber left from past cuts (Turner et al. 1996). In addition, areas that are urbanized are unlikely to be available for any other land uses because urbanization locks in a pattern on the landscape that is hard to reverse. This difficulty of reversal also holds for suburban sprawl and the development of vacation or retirement homes.

The concept of externalities, discussed earlier (see *Land-use decision making in the United States: Private lands*) as a foundation of government's role in private land use and management, needs to be considered within this guideline. Land actions should be implemented with some consideration as to the physical, biological, aesthetic, or economic constraints that are placed on future uses of the land. External effects can extend beyond the boundaries of individual ownership and thus have the potential to affect surrounding owners.

Planning for the long term requires consideration of the potential for unexpected events, such as variations in temperature or precipitation patterns or disturbances. Although disturbances shape the characteristics of ecosystems, estimating the occurrence and implications of these unanticipated events is difficult. Nevertheless, land-use plans must include them. For example, the western coast of the United States has a high potential for volcanic eruption, which would have severe effects. Yet, predicting exact impacts is not possible. Climate change is occurring, but global-climate-projection models cannot determine the temperature and precipitation changes that will happen in any one place. Thus, potential impacts of land-use changes on future dynamics should be recognized but cannot be precisely

specified, as yet. Similarly, land-use changes that affect natural water drainages can cause catastrophic flooding during extreme rain events (Sparks 1996). Although it will not be possible to foresee all extreme events or the effects of a land-use decision on natural variations, it is important to estimate likely changes.

Long-term planning must also recognize that one cannot simply extrapolate historical land-use impacts forward to predict future consequences of land use. The transitions of land from one use or cover type to another often are not stable from one period to another (Turner et al. 1996, Wear et al. 1996) because of changes in demographics, public policy, market economies, and technological and ecological factors. Thus, models produce projections of potential scenarios rather than predictions of future events. It is difficult to model (or even understand) the full complex of interactions among the factors that determine land-use patterns, yet models offer a useful tool to consider potential long-term and broad-scale implications of land-use decisions.

Preserve rare landscape elements and associated species

Rare landscape elements often provide critical habitats. For example, in the Southern Appalachian Mountains, 84% of the federally listed terrestrial plant and animal species occur in rare communities (Southern Appalachian Assessment 1996). While these communities occupy a small area of land, they contain features important for the region's biological diversity. Therefore, rare landscape elements need to be identified, usually via an inventory and analysis of vegetation types, hydrology, soils, and physical features that identifies the presence and location of rare landscape elements and, when possible, associated species (e.g., see Mann et al. 1999). Once the inventory is complete, effects of alternative land-use decisions on these landscape elements and species can be estimated. These effects can then be considered in view of the overall goal for the project, the distribution of elements and species across the landscape, and their susceptibility, given likely future land changes in the vicinity and region. Strategies to avoid or mitigate serious impacts can then be developed and implemented. This guideline to preserve rare landscape elements and associated species derives from both the species and place principles.

Avoid land uses that deplete natural resources over a broad area

Depletion of natural resources disrupts natural processes in ways that often are irreversible over long periods of time. The loss of soil via erosion that occurs during agriculture and the loss of wetlands and their associated ecological processes and species are two

examples. This guideline entails prevention of the rapid or gradual diminishment of resources, such as water or soil. This task first requires the determination of resources at risk. For example, in the southwestern United States, water might be the most important resource; but elsewhere, water might not be a limiting factor, yet it may not be readily replaced. Evaluation of whether a resource is at risk is thus an ongoing process as the abundance and distribution of resources change.

This guideline also calls for the deliberation of ways to avoid actions that would jeopardize natural resources. Some land actions are inappropriate in a particular setting or time, and they should be avoided. Examples of inappropriate actions are farming on steep slopes, which might produce soil loss; logging on stream sides, which may jeopardize the habitat for aquatic organisms; and growing hydrophilic plants in areas that require substantial watering (e.g., lawns grown in arid areas).

Retain large contiguous or connected areas that contain critical habitats

Large areas are often important to maintaining key organisms and ecosystem processes (e.g., Brown 1978, Newmark 1995). Habitats are places on the landscape that contain the unique set of physical and biological conditions necessary to support a species or guild. Thus, the features of a habitat must be interpreted in the context of the species or community that defines them. Habitat becomes critical to the survival of a species or population when it is rare or disconnected. Thus, this guideline derives from both the place and landscape principles. Size and connectivity of patches provide ecological benefits. The presence of animals in an area can be predicted by the size of their home range and their ability to cross gaps of inhospitable habitat (Dale et al. 1994b, Mladenoff 1995, Box 6). However, habitat connectivity is not always a positive attribute for species and ecosystems. Land uses that serve as barriers to species' movement can have long-term negative effects on populations (e.g., Merriam et al. 1989); but, at the same time, corridors can facilitate the spread of nonnative species or diseases. (See the next guideline, below.) Additionally, habitats do not need to be in natural areas to provide benefits for wildlife. For example, golf courses in the southeastern United States often contain enough long-leaf pine (*Pinus palustris*) to provide habitat for the endangered Red-cockaded Woodpecker (*Picooides borealis*).

Again, the importance of spatial connections depends on the priorities and elements of a situation. A first step in implementing the guideline is to examine the spatial connectivity of key habitats in an area, determining which patches are connected and whether the connectivity has a temporal component. Second, op-

portunities for connectivity must be promoted. Sometimes, those opportunities complement other planning needs. For instance, corridors along streams must be protected during timber extraction to provide benefits for aquatic species (Naiman and Décamps 1997).

The term "connected" also should be defined in a manner specific to the situation. In some cases, two areas that are divided by a land-cover type may be artificially connected. For example, the habitat of panther (*Felis concolor coryi*) that is bisected by roads in Florida is now connected by tunnels under the highway (Foster and Humphrey 1995). For other species, such as meadow voles (*Microtus pennsylvanicus*), roadside vegetation itself serves as a corridor between habitat sites (see Getz et al. 1978). In other cases, areas of similar habitat need not be directly adjacent but only need to be within the dispersal distance of the species of concern (e.g., migratory birds returning to nesting grounds [Robinson et al. 1995]). The connections provided by linear land-cover features, such as roads, may have both positive and negative effects (Forman and Alexander 1998), and thus the broad-scale impacts of these features require careful consideration.

Minimize the introduction and spread of nonnative species

The species principle indicates that nonnative organisms often have negative effects on native species and the structure and functioning of ecological systems. Thus, land-use decisions must consider the potential for the introduction and spread of nonnative species. Land planning should consider vehicle movement along transportation routes, the planting of native species, and control of pets. For example, transportation routes have been very important in the spread of the spores of the pathogen *Phytophthora lateralis*, which kills Port Orford cedar (*Chamaecyparis lawsoniana*), an important timber species of southwestern Oregon (Harvey et al. 1985, Zobel et al. 1985). The USDA Forest Service has found that cleaning trucks or minimizing traffic during wet periods can dramatically reduce the transport of this pathogen between forests. Similarly, the spread of gypsy moth (*Lymantria dispar*) is correlated with overseas transportation of the eggs, larvae, and adults in the cargo holds of ships (Hofacker et al. 1993) or along roads when egg sacs are attached to vehicles (Sharov et al. 1997) or outdoor furniture. The great potential for vehicular transport of nonnative species was demonstrated by a case in which material was collected from the exterior surface of an automobile following a drive through central Europe; the collected matter represented 124 plant species and exhibited a high proportion of foreign propagules (Schmidt 1989). The introduction of aquatic organisms transported incidentally with shipping traffic is a com-

parable example for aquatic ecosystems. Many of these introductions have had devastating effects. Waterways for shipping have impacts on the movement of introduced species not unlike those of roadways.

Often, growing native species reduces the need for planting nonnative species, particularly in urban, suburban, or other developed areas. The planted native species can then provide propagules that may disperse and establish. As an added benefit, the native species are adapted to the local conditions and frequently become established more readily and require less maintenance than nonnatives. Native species are also adapted to long-term variations in climate or disturbance regimes to which nonnative species often succumb. Terrestrial environmental conditions associated with native vegetation may also deter the spread of nonnatives. For example, in small forest islands interspersed among alien-dominated agroecosystems in Indiana, even the smallest forest remnants retained interior habitat conditions sufficient to resist invasion by the available nonnative plant species (Brothers and Spingharn 1992). Introduced agricultural crops often result in less sustainable farming practices than does the use of native crops, as has been observed in the Brazilian Amazon (Soulé and Piper 1992).

The control of pets is an essential aspect of reducing introductions. As suburbanization expands, one of the major effects on native fauna is the introduction of exotic pets. The mosquitofish (*Gambusia affinis*), swordtail (*Xiphophorus helleri*), and other species used as pets and then released into the wild have had a dramatic impact on the native fauna (Gamradt and Kats 1996). In addition, cats (*Felis catus*) kill birds and small mammals (Dunn and Tessaglia 1994). In Australia, conservationists have worked with developers and the public to ban dogs from suburban development projects that contain koala habitat because dogs strongly contribute to koala mortality in developed areas.

Avoid or compensate for effects of development on ecological processes

Negative impacts of development might be avoided or mitigated by some forethought. To do so, potential impacts need to be examined at the appropriate scale. At a fine scale, the design of a structure may interrupt regional processes. For example, dispersal patterns may be altered by a road, migrating birds may strike the reflective surfaces of a building, or fish may be entrained in a hydroelectric generator. At a broad scale, patterns of watershed processes may be altered, for example, by changing drainage patterns as part of the development.

Therefore, how proposed actions might affect other systems (or lands) should be examined. For example, landslides are generally site specific so that develop-

ment of places with a high potential for landslides should be avoided. Also, human uses of the land should avoid structures and uses that might have a negative impact on other systems; at the very least, ways to compensate for those anticipated effects should be determined. It is useful to look for opportunities to design land use to benefit or enhance the ecological attributes of a region. For example, golf courses can be designed to serve as wildlife habitat (Terman 1997), or traffic in rural areas can be concentrated on fewer and more strategically placed roads, resulting in decreased traffic volumes and flows within the region as a whole and less impact on wildlife (Jaarsma 1997).

Implement land-use and land-management practices that are compatible with the natural potential of the area

The place principle implies that local physical and biotic conditions affect ecological processes. Therefore, the natural potential for productivity and for nutrient and water cycling partially determine the appropriate land-use and land-management practices for a site. Land-use practices that fall within these limits are usually cost effective in terms of human resources and future costs caused by unwarranted changes on the land. Nevertheless, supplementing the natural resources of an area by adding nutrients through fertilization or water via irrigation is common. Even with such supplements, however, the natural limitations of the site must be recognized for cost-effective management. Implementing land-use and land-management practices that are compatible with the natural potential of the area requires that land managers have an understanding of the site potential. Traditional users of the land (e.g., native farmers) typically have a close relationship with the land. As farming and other resource extraction become larger and more intensive, the previous close association that managers had with the land is typically lost. Yet, land-management practices such as no-till farming reduce soil erosion or mitigate other resource losses. Often, however, land uses ignore site limitations or externalize site potential. For example, building shopping malls on prime agriculture land does not make the best use of the site potential. Also, establishing farms where irrigation is required or lawns where watering is necessary assumes that site constraints will be surmounted. Nevertheless, the land products are still limited by the natural potential of the site.

THE FUTURE: PREDICTIONS, UNCERTAINTIES,
AND SURPRISES

Land use in a future world

This paper began with a challenge for land use and management: to address the conflicting goals and de-

sires for use of the land. To meet this challenge, ecological principles and their implications were identified, current processes for making land-use decisions were discussed, and guidelines were proposed for improving the process and for identifying the long-term effects on the landscape. Nevertheless, societies will continue to impose additional and increasingly complex impacts on the land. Environmental changes in the future will be driven by population growth and urbanization, economic expansion, resource consumption, technological development, and environmental attitudes and institutions (EPA 1995, Naiman et al. 1998). Despite these pressures, further poorly planned land-use changes and their ecological consequences are not predestined or inevitable. Rather, policymakers will shape the future landscape, and scientists have a significant opportunity to help guide that process for the benefit of all creatures.

Predicting future patterns in land use requires knowledge of changing human demographics and patterns of resource consumption. For example, the aging of the U.S. population and the pending retirement surge among the baby-boom generation is likely to have a strong impact on patterns of settlement and recreation. The development of urban centers that will result from relocation patterns of humans should also be considered. Uncertainties abound regarding the future consumptive patterns and environmental attitudes of demographically influential segments of the population, and these uncertainties are likely to lead to surprises.

Patterns of our future landscapes will result not only from changes in land use but also from other broad-scale changes, especially those resulting from global warming (Santer et al. 1996). The implications of global climate change are profound for water availability, for the probability of natural-disturbance events such as fires or floods, and for the production of food and fiber (Watson et al. 1998). Because regional projections of climate change are uncertain, the implications of climate change for land-use patterns remain unclear. However, planning for future land uses should not be conducted under the assumption that today's climate and environmental conditions will persist, unaltered, into the future. The likelihood of substantial environmental changes should be considered in alternative future scenarios; lack of attention to such changes may result in land uses that are incompatible with future environmental conditions (e.g., increased density of residential development in locations where fire frequency will increase). In turn, patterns of land cover and the degree of fragmentation of natural habitats will influence the ability of ecological systems to respond to a changing climate. The interactions between land-use patterns and climate change are complex (Dale 1997).

Emerging technologies that may change land-use and land-management practices or moderate deleterious effects

Examination of recent history provides many examples of how the emergence of new technologies has profoundly affected societal use of the landscape (Headrick 1990). Inventions, such as powerful water pumps, labor-saving machinery, and the development of herbicides and pesticides, have fundamentally altered agriculture and forestry; construction of highways and river locks have forever altered the transportation and use of essential goods; and medical advances have reshaped the age structure and size of human populations. New technologies continue to emerge, and some will have strong influences either on the distribution of human populations or on land use. We offer two examples.

Telecommunications and the virtual office.—Recent and emerging advances in telecommunications promise to change the way business is conducted and thereby influence patterns of human settlement. The spatial dispersion of human settlement will likely increase as proximity to urban centers or corporate offices becomes less critical. Professionals conducting business via electronic mail or the Internet may choose to live farther from urban centers on relatively larger home sites. Road density of rural areas and ownership of 1- to 3-ha parcels will likely increase, which could exacerbate (1) nonpoint-source erosion and nutrient pollution from intensive land use by domestic animals (horses, cattle, and sheep) and (2) the introduction of nonnative species. Exact patterns and uses are difficult to predict, but it is likely that widespread implementation of new telecommunication technologies will affect land patterns and uses.

Natural-resource utilization.—Future increases in the use of natural resources will place demands on the land base. Emerging technologies targeted at more efficient resource production (e.g., food and fiber) and water use have the potential to minimize the deleterious effects of these demands; yet, projecting the outcomes on land use and land cover is difficult. As examples, consider emerging trends in fiber production and water use.

Global demand for wood-based products continues to increase (FAO 1997). Some likely results of this rise in demand are:

- 1) extensive tracts of previously unexploited forests will be cut;
- 2) managed forests will be cut on shorter rotations
- 3) plantation areas will increase; or
- 4) effective uses will be found for fiber that is currently not utilized.

Indeed, extensive tracts of previously unexploited for-

ests in the former Soviet Union and in tropical regions are being harvested for the first time (FAO 1997), and yield from managed industrial forests is being optimized. In addition, research efforts in the forest-products industry are directed at improving other uses of wood and fiber particles that require only wood chips and plant fragments, implying less waste and an increased use of other plant fragments in building materials. Technologies are also being developed to harvest trees in a more environmentally sound manner. Each of these possible avenues will have long-term effects on land use, although the chosen path will depend on patterns in wood-resource availability and demand.

Technologies are already available to improve substantially the efficiencies of water and energy use with concomitant impacts on the land (McKinney and Schoch 1996). In the United States, where agriculture is a large user of water, microirrigation is slowly gaining a foothold, especially in western regions where water is limited and the environmental costs of food production are high. In addition, conservation advances in personal water use include low-flush toilets, low-volume shower heads, and home landscaping designed for the climate. Collectively, these technological changes, along with behavioral adjustments, indicate that water-use impacts on the land will be different in the future.

Making sustained progress

Much progress has been made in managing land in ecologically sustainable ways. Often, these gains are made as a result of past mistakes. For example, in the aftermath of the Dust Bowl in the Great Plains of the United States, crops more compatible with site conditions were grown, and trees were planted in rows to provide windbreaks. Even so, as the memory of the Dust Bowl faded, unsustainable land-management practices returned, and more soil has been lost in recent dust storms.

Instead of just learning from past mistakes at a site, it is possible to synthesize the lessons from ecological science that relate to land use. This paper presents ecological principles relevant to land use and management and develops them into guidelines for use of the land. However, more actions are needed before ecologically based land management is broadly implemented. These guidelines must be translated to particular land uses. This translation can be done, for example, by using the principles and guidelines to shape municipal ordinances for land use practices. In addition, the guidelines can provide the basis for specifying and understanding ecological concerns relevant to the needs of specific types of land users, such as farmers or foresters.

Another important step in this process is to set sci-

entifically based priorities for developing the ecological science necessary to meet the needs of land-use management. Unfortunately, the priorities are lacking at present. Other fields in environmental and human sciences have set priorities that have helped to shape their disciplines (Lubchenco et al. 1991, NRC 1994, Naiman et al. 1995). It is important that ecologists, land planners, and decision makers (1) define priorities to sustain progress in developing the science needed by land managers and (2) revise them on a regular basis to reaffirm that these priorities are still valid.

Therefore, we propose five actions to develop the science that is needed by land managers:

- 1) Apply ecological principles to land use and land management.
- 2) Explore ecological interactions in both pristine and heavily used areas.
- 3) Develop spatially explicit models that integrate social, economic, political, and ecological land-use issues.
- 4) Improve the use and interpretation of in situ and remotely sensed data to better understand and predict environmental changes and to monitor the environment.
- 5) Communicate relevant ecological science to users (which includes land owners and the general public).

This paper does not address the environmental, social, economic, and political trade-offs that often occur in setting land policy (Kindler 1998). Trade-offs are often based on subjective value judgments reflecting economic, social, cultural, and aesthetic preferences accorded by a society to different objectives. For example, consideration of such trade-offs are central components of land-use agreements in the restoration of the Everglades (Harwell 1997) and in developing options for fisheries and ancient forests in the Pacific Northwest (Kohm and Franklin 1997). However, this observation highlights an important issue in land-use management: What is the role of science in the decision process?

Society and the ecological community have not yet converged on a mechanism for incorporating science into land-use policy. Positive steps in integrating scientific ideas and land-use management are being taken at the international scale, as demonstrated by the Rio Accord of 1992 and the Kyoto Protocol of 1997, and at the national scale, as evidenced by the U.S. Man and the Biosphere Program (Harwell 1997), the Sustainable Biosphere Initiative (Lubchenco et al. 1991), the formulation of ecosystem-management guidelines (Christensen et al. 1996), practical land-management approaches for the forests of the Pacific Northwest (FEMAT 1993) and for the national forests (Committee of Scientists 1999), and a host of studies by the National Research Council (Policansky 1998). At the local scale,

watershed alliances and other types of nongovernmental organizations (NGOs) have experienced an unprecedented increase in numbers in response to the perception that government agencies are not doing enough to manage the land sustainably (von Hagen et al. 1998). In each case, science is only a part of the solution, although an essential part. Researchers and policy analysts recognize that most land-management decisions currently have little relation to ecological science, being influenced more strongly by economics, values, traditions, politics, and other factors. If ecological science is to guide land use and land management and to have a positive impact on resources and people, it must be clearly and reliably communicated. This requires scientists to identify relevant scientific issues and explain the importance of those issues within the decision-making process.

ACKNOWLEDGMENTS

Comments on an earlier draft were provided by Joan Baker, Jill Baron, Ingrid Burke, Richard Forman, Jerry Franklin, Norm Johnson, Lou Pitelka, Clay Montague, Patricia Parr, Emily Russell, Thomas Stohlgren, Tom Wilbanks, and four anonymous reviewers. Discussions with Barry Noon were helpful. Fred O'Hara and Linda O'Hara edited the paper, and Jeannette Cox assisted with the references and figures. The development of this paper was funded by the Environmental Protection Agency and the National Aeronautics and Space Administration through the Sustainable Biosphere Initiative of the Ecological Society of America. This paper is Environmental Sciences Division Publication number 4840 of Oak Ridge National Laboratory, which is managed by Lockheed Martin Energy Research Corporation for the Department of Energy under contract DE-AC05-96OR22464. This paper has been authored by a contractor of the U.S. Government under contract No. DE-AC05-96OR22464. Accordingly, the U.S. Government retains a nonexclusive, royalty-free license to publish or reproduce the published form of this contribution, or to allow others to do so, for U.S. Government purposes.

LITERATURE CITED

- Albrecht, V., J. Barone, R. C. Einsweiler, H. Grossman, W. Hare, R. Lilieholm, W. K. Olson, T. Quimby, A. Randall, and C. Whiteside. 1995. Managing land as ecosystem and economy. Lincoln Institute of Land Policy, Cambridge, Massachusetts, USA.
- Andren H. 1997. Population response to landscape changes depends on specialization to different landscape elements. *Oikos* **80**:193–196.
- Baker, W. L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology* **73**:1879–1887.
- Belknap, W. C., and R. J. Naiman. 1998. A GIS and TIR procedure to detect and map wall-base channels in western Washington. *Journal of Environmental Management* **52**:147–160.
- Bilby, R. E., and P. A. Bisson. 1998. Function and distribution of large woody debris. Pages 324–346 in R. J. Naiman and R. E. Bilby. *River ecology and management*. Springer-Verlag, New York, New York, USA.
- Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* **64**:369–400.
- Bossleman, F., and D. Callies. 1972. The quiet revolution in land use control. Council on Environmental Quality, Washington, D.C., USA.
- Brothers, T. S., and A. Spingharn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* **6**:91–100.
- Brown, J. H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist Memoirs* **2**:209–227.
- Burgess, R. L., and D. M. Sharpe, editors. 1981. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Busch, D. E., and S. D. Smith. 1995. Mechanisms associated with the decline of woody species in riparian ecosystems of the southwestern U.S. *Ecological Monographs* **65**:347–370.
- Caldwell, L. K., and K. Shrader-Fechette. 1993. *Policy for land: law and ethics*. Rowan and Littlefield, Lanham, Maryland, USA.
- Callies, D. L. 1994. *Preserving paradise: why regulations won't work*. University of Hawaii Press, Honolulu, Hawaii, USA.
- Carpenter, S. R. 1992. Destabilization of planktonic ecosystems and blooms of blue-green algae. Pages 461–481 in J. F. Kitchell, editor. *Food web management*. Springer-Verlag, New York, New York, USA.
- Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity. *Bioscience* **38**:764–769.
- Carroll, C. R., J. H. Vandermeer, and P. M. Rosset, editors. 1990. *Agroecology*. McGraw-Hill, New York, New York, USA.
- Chabot, B. F., and H. A. Mooney, editors. 1985. *Physiological ecology of North American plant communities*. Chapman & Hall, New York, New York, USA.
- Charbonneau, R., and G. M. Kondolf. 1993. Land use change in California, USA: nonpoint source water quality impacts. *Environmental Management* **17**:453–460.
- Christensen, N. L., A. M. Bartuska, J. H. Brown, S. R. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, D. J. Parsons, C. H. Peterson, M. G. Turner, and R. G. Woodmansee. 1996. The report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* **6**:665–691.
- Committee of Scientists. 1999. *Sustaining the people's lands: recommendations for stewardship of the national forests and grasslands into the next century*. U.S. Department of Agriculture, Washington, D.C., USA.
- Conner, R. N., and D. C. Rudolph. 1991. Effects of midstory reduction and thinning in Red-cockaded Woodpecker cavity tree clusters. *Wildlife Society Bulletin* **19**:63–66.
- Cowles, H. C. 1911. The causes of vegetation cycles. *Botanical Gazette* **51**:161–183.
- Cullingworth, B. 1997. *Planning in the USA: policies, issues, and processes*. Routledge, London, UK.
- Dale, V. H. 1997. The relationship between land-use change and climate change. *Ecological Applications* **7**:753–769.
- Dale, V. H., A. E. Lugo, J. A. MacMahon, and S. T. A. Pickett. 1998. Management implications of large, infrequent disturbances. *Ecosystems* **1**:546–557.
- Dale, V. H., L. K. Mann, R. J. Olson, D. W. Johnson, and K. C. Dearstone. 1990. The long-term influence of past land use on the Walker Branch forest. *Landscape Ecology* **4**:211–224.
- Dale, V. H., R. V. O'Neill, M. Pedlowski, and F. Southworth. 1993. Causes and effects of land-use change in central Rondônia, Brazil. *Photogrammetric Engineering and Remote Sensing* **56**:997–1005.

- Dale, V. H., R. V. O'Neill, F. Southworth, and M. Pedlowski. 1994a. Modeling effects of land management in the Brazilian amazonian settlement of Rondônia. *Conservation Biology* **8**:196–206.
- Dale, V. H., S. M. Pearson, H. L. Offerman, and R. V. O'Neill. 1994b. Relating patterns of land-use change to faunal biodiversity in the central Amazon. *Conservation Biology* **8**:1027–1036.
- DeFerrari, C., and R. J. Naiman. 1994. A multiscale assessment of exotic plants on the Olympic Peninsula, Washington. *Journal of Vegetation Science* **5**:247–258.
- DeGrove, J. M. 1992. Planning and growth management in the states. Lincoln Institute of Land Policy, Cambridge, Massachusetts, USA.
- Dennis, J. V. 1971. Species using Red-cockaded Woodpecker holes in northeastern South Carolina. *Bird-Banding* **42**:79–87.
- Detenbeck, N. E., C. A. Johnston, and G. J. Niemi. 1993. Wetland effects on lake water quality in the Minneapolis/St. Paul metropolitan area. *Landscape Ecology* **8**:39–61.
- Diamond, H. L., and P. F. Noonan. 1996. Land use in America: report of the sustainable use of land project. Island Press, Covelo, California, USA.
- Diamond, J. 1997. Guns, germs, and steel: the fates of human societies. W. W. Norton, New York, New York, USA.
- Diaz, N., and D. Apostol. 1992. Forest landscape analysis and design. Eco-TP-043-92. USDA Forest Service, Pacific Northwest Region, Portland, Oregon, USA.
- Douglas, Ian. 1994. Human settlements. Pages 149–169 in W. B. Meyer and B. L. Turner II, editors. *Changes in land use and land cover: a global perspective*. Cambridge University Press, Cambridge, UK.
- Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. 1989. *Biological invasions: a global perspective*. John Wiley & Sons, Chichester, UK.
- Dunn, E. H., and D. L. Tessaglia. 1994. Predation of birds at feeders in winter. *Journal of Field Ornithology* **65**:8–16.
- EPA [U.S. Environmental Protection Agency]. 1995. Beyond the horizon: using foresight to protect the environmental future. EPA-SAB-EC-95-007. USEPA Science Advisory Board Washington, D.C., USA.
- Eschner, T. R., R. F. Hadley, and K. D. Crowley. 1983. Hydrologic and morphologic changes in channels of the Platte River Basin in Colorado, Wyoming, and Nebraska: a historical perspective. U.S. Geological Survey Professional Paper 1277-A. U.S. Government Printing Office, Washington, D.C., USA.
- Ewel, J. J., M. J. Mazzarino, and C. W. Berish. 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. *Ecological Applications* **1**:289–302.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603–610.
- FAO [Food and Agriculture Organization]. 1993. Forest resources assessment 1990: tropical countries. FAO Forestry Paper 112. United Nations Food and Agriculture Organization, Rome, Italy.
- FAO [Food and Agriculture Organization]. 1996. Forest resources assessment 1990: survey of tropical forest cover and study of change processes. United Nations Food and Agriculture Organization, Rome, Italy.
- FAO [Food and Agriculture Organization]. 1997. State of the world's forests. United Nations Food and Agriculture Organization, Rome, Italy.
- FEMAT [Forest Ecosystem Management Assessment Team]. 1993. *Forest ecosystem management: an ecological, economic, and social assessment*. USDA Forest Service, Washington, D.C., USA.
- Forman, R. T. T. 1995. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**:207–231.
- Foster, D. R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. *Journal of Ecology* **80**:753–772.
- Foster, M. L., and S. R. Humphrey. 1995. Use of highway underpasses by Florida panthers and other wildlife. *Wildlife Society Bulletin* **23**:95–100.
- Frank, D. A., and R. S. Inouye. 1994. Temporal variation in actual evapotranspiration of terrestrial ecosystems: patterns and ecological implications. *Journal of Biogeography* **21**:401–411.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications* **3**:202–205.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* **1**:5–18.
- Gale, D. E. 1992. Eight state-sponsored growth management programs: a comparative analysis. *Journal of the American Planning Association* **58**:425–439.
- Gamradt, S. C., and L. B. Kats. 1996. Effect of introduced crayfish and mosquitofish on California newts. *Conservation Biology* **10**:1155–1162.
- Gardner, R. H., R. V. O'Neill, M. G. Turner, and V. H. Dale. 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. *Landscape Ecology* **3**:217–228.
- Garner, J. F., and D. L. Callies. 1972. Planning law in Wales and the United States. *Anglo-American Law Review* **1**:292–334.
- Getz, L. L., F. R. Cole, and D. L. Gates. 1978. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *Journal of Mammalogy* **59**:208–12.
- Gilruth, P. T., S. E. Marsh, and R. Itami. 1995. A dynamic spatial model of shifting cultivation in the highlands of Guinea, West Africa. *Ecological Modelling* **79**:179–197.
- Givnish, T. J., editor. 1986. *On the economy of plant form and function*. Cambridge University Press, New York, New York, USA.
- Glantz, M. H., editor. 1994. *Drought follows the plow*. Cambridge University Press, New York, New York, USA.
- Glenn-Lewin, D. C., and E. van der Maarel. 1992. Patterns and processes of vegetation dynamics. Pages 11–59 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession*. Chapman & Hall, New York, New York, USA.
- Haeuber, R. A., and W. K. Michener. 1998. Policy implications of recent natural and managed floods. *BioScience* **48**:765–772.
- Hansson, L., L. Fahrig, and G. Merriam, editors. 1995. *Mosaic landscapes and ecological processes*. Chapman & Hall, New York, New York, USA.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**:133–302.
- Harms, W. B., A. H. F. Stortelder, and W. Vos. 1987. Effects of intensification of agriculture on nature and landscape in

- the Netherlands. Pages 357–379 in M. G. Wolman and F. G. Fourier, editors. Land transformation in agriculture. John Wiley & Sons, New York, New York, USA.
- Harvey, R. D., J. S. Hadfield, and H. Greenup. 1985. Port Orford cedar root rot on the Siskiyou National Forest in Oregon. USDA, Forest Service, Forest Insect and Disease Management, Pacific Northwest Region, Portland, Oregon, USA.
- Harwell, M. A. 1997. Ecosystem management of South Florida. *BioScience* **47**:499–512.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical Population Biology* **18**:363–373.
- Headrick, D. R. 1990. Technology change. Pages 5–67 in B. L. Turner II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Matthews, and W. B. Meyer, editors. The earth as transformed by human action: global and regional changes in the biosphere over the past 300 years. Cambridge University Press, Cambridge, UK.
- Hobbs, N. T., and D. S. Schimel. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *Journal of Range Management* **37**:402–205.
- Hofacker, T. H., M. D. South, and M. E. Mielke. 1993. Asian gypsy moths enter North Carolina by way of Europe: a trip report. *Gypsy Moth News* **33**:13–15.
- Houghton, R. A. 1995. Land-use change and the carbon cycle. *Global Change Biology* **1**:275–287.
- Houghton, R. A., D. S. Lefkowitz, and D. L. Skole. 1991. Changes in the landscape of Latin America between 1850 and 1985. I. Progressive loss of forests. *Forest Ecology and Management* **38**:143–172.
- Hunter, W. C., R. D. Ohmart, and B. W. Anderson. 1988. Use of exotic salt cedar (*Tamarisk chinensis*) by birds in arid riparian systems. *Condor* **90**:113–123.
- Inouye, R. S., and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology* **76**:1872–1887.
- IPCC [Intergovernmental Panel on Climate Change]. 1996. Climate change 1995. Impacts, adaptations, and mitigation of climate change: scientific-technical analyses. Cambridge University Press, Cambridge, UK.
- Iverson, L. R. 1991. Forest resources of Illinois: What do we have, and what are they doing for us? *Illinois Natural History Survey Bulletin* **34**:361–374.
- Iverson, L. R., G. L. Rolfe, T. J. Jacob, A. S. Hodges, and M. R. Jeffords. 1991. Forests of Illinois. Illinois Council on Forestry Development, Urbana, Illinois, USA.
- Jaarsma, C. F. 1997. Approaches for the planning of rural road networks according to sustainable land-use planning. *Landscape and Urban Planning* **39**:47–54.
- Jennersten, O. 1988. Pollination in *Dianthus deltooides* (*Caryophyllaceae*): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* **2**:359–366.
- Johansen, C. A. 1977. Pesticides and pollinators. *Annual Review of Entomology* **22**:177–192.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**:373–386.
- Kates, R. W., W. C. Clark, V. Norberg-Bohm, and B. L. Turner II. 1990. Human sources of global change: a report on priority research initiatives for 1990–1995. Discussion paper G-90–08. Global Environmental Policy Project, John F. Kennedy School of Government, Harvard University, Cambridge, Massachusetts, USA.
- Kearns, C. A., and D. W. Inouye. 1997. Pollinators, flowering plants, and conservation biology. *BioScience* **47**:297–307.
- Kindler, J. 1998. Linking ecological and development objectives: trade-offs and imperatives. *Ecological Applications* **8**:591–600.
- Knopf, F. L. 1986. Changing landscapes and the cosmopolitanism of the eastern Colorado avifauna. *Wildlife Society Bulletin* **14**:132–142.
- Knopf, F. L., and F. B. Samson. 1994. Scale perspectives of avian diversity in western riparian ecosystems. *Conservation Biology* **8**:669–676.
- Knopf, F. L., and M. L. Scott. 1990. Altered flows and created landscapes in the Platte River headwaters, 1840–1990. Pages 47–70 in J. M. Sweeney, editor. Static management of dynamic ecosystems. Wildlife Society, West Lafayette, Indiana, USA.
- Kohm, K. A., and J. F. Franklin. 1997. Creating a forestry for the 21st century. Island Press, Covelo, California, USA.
- Kunstler, J. H. 1993. The geography of nowhere: the rise and decline of America's man-made landscape. Simon & Schuster, New York, New York, USA.
- Lamont, B. B., P. G. L. Klinkhamer, and E. T. F. Witkowski. 1993. Population fragmentation may reduce fertility to zero in *Banksia goodii*: a demonstration of the Allee effect. *Oecologia* **94**:446–450.
- Lee, R. G., R. O. Flamm, M. G. Turner, C. Bledsoe, P. Changler, C. DeFerrari, R. Gottfried, R. J. Naiman, N. Schumaker, and D. Wear. 1992. Integrating sustainable development and environmental vitality. Pages 499–521 in R. J. Naiman, editor. New perspectives in watershed management. Springer-Verlag, New York, New York, USA.
- Liu, D. S., L. R. Iverson, and S. Brown. 1993. Rates and patterns of deforestation in the Philippines: application of geographic information system analysis. *Forest Ecology and Management* **57**:1–16.
- Loomis, J. B. 1996. Integrated public lands management: principles and applications to national forests, parks, wildlife refuges and BLM lands. Columbia University Press, New York, New York, USA.
- Lovejoy, T. E., R. O. Bierregard, A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, A. V. H. Powell, H. O. R. Schubert, and M. B. Hays. 1986. Edge and other effects of isolation on Amazonian forest fragments. Pages 257–285 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts, USA.
- Lubchenco, J. A., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, and P. G. Riser. 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* **72**:371–412.
- Lugo, A. E. 1991. Cities in the sustainable development of tropical landscapes. *Nature and Resources* **27**:27–35.
- Lugo, A. E., and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* **28**:585–599.
- Mahlman, J. D. 1997. Uncertainties in projections of human-caused climate warming. *Science* **278**:1416–1417.
- Mann, L. K., A. W. King, V. H. Dale, W. W. Hargrove, R. Washington-Allen, L. Pounds, and T. A. Ashwood. 1999. The role of soil classification in GIS modeling of habitat pattern: threatened calcareous ecosystems. *Ecosystems* **2**:524–538.
- McKinney, M. L., and R. M. Schoch. 1996. Environmental science. Jones and Bartlett, Sudbury, Massachusetts, USA.
- McNaughton, S. J. 1979. Grassland-herbivore dynamics. Pages 46–81 in A. R. E. Sinclair and M. Norton-Griffiths,

- editors. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.
- McNaughton, S. J. 1993. Biodiversity and function of grazing ecosystems. Pages 361–383 in E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.
- Mech, L. D., S. H. Fritts, and D. Wagner. 1995. Minnesota wolf dispersal to Wisconsin and Michigan. *American Midland Naturalist* **105**:408–409.
- Merriam, G., M. Kozakiewicz, E. Tsuchiya, and K. Hawley. 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. *Landscape Ecology* **2**:227–35.
- Meyer, W. B., and B. L. Turner II. 1992. Human population growth and global land-use/cover change. *Annual Review of Ecology and Systematics* **23**:39–61.
- Meyer, W. B., and B. L. Turner II, editors. 1994. Changes in land use and land cover: a global perspective. Cambridge University Press, Cambridge, UK.
- Milchunas, D. G., and W. K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. *Ecological Applications* **5**:452–458.
- Miller, J. R., T. T. Schultz, N. T. Hobbs, K. R. Wilson, D. L. Schrupp, and W. L. Baker. 1995. Changes in the landscape structure of a southeastern Wyoming riparian zone following shifts in stream dynamics. *Biological Conservation* **72**:371–379.
- Mitchell, R. 1984. The ecological basis for comparative primary productivity. Pages 13–53 in R. Lowrance, B. R. Stinner, and G. J. House, editors. *Agricultural ecosystems*. Wiley Interscience, New York, New York, USA.
- Mladenoff, D. J., R. G. Haight, T. A. Sickley, and A. P. Wydeven. 1997. Causes and implications of species restoration in altered ecosystems. *BioScience* **47**:21–31.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* **9**:279–294.
- Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. *Ecological Monographs* **66**:345–365.
- Nabhan, G. P. 1982. *The desert smells like rain: a naturalist in Papago Indian country*. North Point Press, San Francisco, California, USA.
- Nabhan, G. P. 1986. *Gathering the desert*. University of Arizona Press, Tucson, Arizona, USA.
- Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* **28**:621–658.
- Naiman, R. J., J. J. Magnuson, and P. L. Firth. 1998. Integrating cultural, economic and environmental requirements for fresh water. *Ecological Applications* **8**:569–570.
- Naiman, R. J., J. J. Magnuson, D. M. McKnight, and J. A. Stanford, editors. 1995. *The freshwater imperative: a research agenda*. Island Press, Washington, D.C., USA.
- Naiman, R. J., and K. H. Rogers. 1997. Large animals and system-level characteristics in river corridors. *BioScience* **47**:521–529.
- Newmark, W. D. 1995. Extinction of mammal populations in western North American National Parks. *Conservation Biology* **9**:512–525.
- Noss, R. F., and B. Csuti. 1994. Habitat fragmentation. Pages 237–264 in G. K. Meffe and C. R. Carroll, editors. *Principles of conservation biology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Noss, R. F., and R. L. Peters. 1995. *Endangered ecosystems: a status report on America's vanishing habitat and wildlife*. Defenders of Wildlife, Washington, D.C., USA.
- NRC [U.S. National Research Council]. 1994. *Setting priorities for the human dimensions of global change*. National Academy Press, Washington, D.C., USA.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* **164**:262–270.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* **103**:91–93.
- Paine, R. T. 1995. A conversation on refining the concept of keystone species. *Conservation Biology* **9**:962–964.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises: everything else is business as usual. *Ecosystems* **1**:535–545.
- Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. *Conservation Biology* **1**:323–334.
- Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecology* **8**:3–18.
- Pearson, S. M., M. G. Turner, R. H. Gardner, and R. V. O'Neill. 1996. An organism-based perspective of habitat fragmentation. Pages 77–95 in R. C. Szaro, editor. *Biodiversity in managed landscapes: theory and practice*. Oxford University Press, New York, New York, USA.
- Peet, R. K. 1992. Community structure and ecosystem function. Pages 103–151 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen. *Plant succession—theory and prediction*. Chapman & Hall, New York, New York, USA.
- Perlin, J. 1989. *A forest journey: the role of wood in the development of civilization*. Harvard University Press, Cambridge, Massachusetts, USA.
- Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology* **65**:1466–75.
- Pickett, S. T. A., and M. L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* **269**:331–334.
- Pickett, S. T. A., S. C. Collins, and J. J. Armesto. 1987a. Models, mechanisms, and pathways of succession. *Botanical Review* **53**:335–371.
- Pickett, S. T. A., S. C. Collins, and J. J. Armesto. 1987b. A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* **69**:109–114.
- Pickett, S. T. A., and P. S. White, editors. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, New York, USA.
- Pimentel, D., H. Acquay, M. Biltonen, P. Rice, M. Silva, J. Nelson, V. Lipner, S. Giordana, A. Horowitz, and M. D'Amore. 1992. Environmental and economic costs of pesticide use. *BioScience* **42**:750–760.
- Platt, R. H. 1996. *Land use and society*. Island Press, Washington, D.C., USA.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* **47**:769–784.
- Policansky, D. 1998. Science and decision making for water resources. *Ecological Applications* **8**:610–618.
- Polis, G. A., and K. O. Winemiller. 1996. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York, New York, USA.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* **73**:733–746.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco,

- and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* **46**:609–620.
- Pulliam, H. R., J. B. Dunning, and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* **2**:165–177.
- Reice, S. R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist* **82**:424–435.
- Richards, J. F. 1990. Land transformations. Pages 163–178 in B. L. Turner II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Matthews, and W. B. Meyer, editors. *The earth as transformed by human action: global and regional changes in the biosphere over the past 300 years*. Cambridge University Press, New York, New York, USA.
- Richards, J. F., and E. P. Flint. 1994. A century of land-use change in south and southeast Asia. Pages 15–66 in V. H. Dale, editor. *Effects of land-use change on atmospheric CO₂ concentrations*. Springer-Verlag, New York, New York, USA.
- Riebsame, W. E., W. J. Parton, K. A. Galvin, I. C. Burke, L. Bohren, R. Young, and E. Knop. 1994. Integrated modeling of land use and cover change. *BioScience* **44**:350–356.
- Risser, P. G. 1985. Toward a holistic management perspective. *BioScience* **35**:414–418.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**:1987–1990.
- Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* **93**:25–30.
- Romme, W. H., and D. G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience* **39**:695–699.
- Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pages 52–65 in R. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. Chicago University Press, Chicago, Illinois, USA.
- Rowcliffe, J. M., A. R. Watkinson, W. J. Sutherland, and J. A. Vickery. 1995. Cyclic winter grazing patterns in Brent Geese and the regrowth of salt-marsh grass. *Functional Ecology* **9**:931–941.
- Rudolph, D. C., and R. N. Conner. 1991. Cavity tree selection by Red-cockaded Woodpeckers in relation to tree age. *Wilson Bulletin* **103**:458–467.
- Santer, B. D., K. E. Taylor, T. M. L. Wigley, T. C. Johns, P. D. Jones, D. J. Karoly, J. F. B. Mitchell, A. H. Oort, J. E. Penner, V. Ramaswamy, M. D. Schwarzkopf, R. J. Stouffer, and S. Tett. 1996. A search for human influences on the thermal structure of the atmosphere. *Nature* **382**:39–46.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**:18–32.
- Scatena, F. N., S. Moya, C. Estrada, and J. D. Chinea. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* **28**:424–440.
- Schmidt, W. 1989. Plant dispersal by motor cars. *Vegetatio* **80**:147–152.
- Schullery, P. 1989. The fires and fire policy. *BioScience* **39**:686–694.
- Schwartz, M. W., editor. 1997. *Conservation in highly fragmented landscapes*. Chapman & Hall, New York, New York, USA.
- Sears, P. B. 1980. *Deserts on the march*. University of Oklahoma Press, Norman, Oklahoma, USA.
- Sessions, J., G. Reeves, K. N. Johnson, and K. Burnett. 1997. Implementing spatial planning in watersheds. Pages 271–283 in K. A. Kohm and J. F. Franklin, editors. *Creating a forestry of the 21st Century*. Island Press, Washington, D.C., USA.
- Sharov, A. A., A. M. Liebhold, and E. A. Roberts. 1997. Correlation of counts of gypsy moths (*Lepidoptera, Lymantriidae*) in pheromone traps with landscape characteristics. *Forest Science* **43**:483–490.
- Smith, H. H. 1993. *The citizen's guide to planning*. American Planning Association, Chicago, Illinois, USA.
- Soranno, P. A., S. L. Hubler, S. R. Carpenter, and R. C. Lathrop. 1996. Phosphorus loads to surface waters: a simple model to account for spatial pattern of land use. *Ecological Applications* **6**:865–878.
- Soulé, J., and J. Piper. 1992. *Farming in nature's image*. Island Press, Washington, D.C., USA.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353–391.
- Southern Appalachian Assessment. 1996. *The Southern Appalachian assessment: summary report*. USDA Forest Service, Washington, D.C., USA.
- Southworth, F., V. H. Dale, and R. V. O'Neill. 1991. Contrasting patterns of land use in Rondônia, Brazil: simulating the effects on carbon release. *International Social Sciences Journal* **130**:681–698.
- Sparks, R. E. 1996. Ecosystem effects: positive and negative outcomes. Pages 132–162 in S. A. Changnon, editor. *The great flood of 1993: causes, impacts, and responses*. Westview, Boulder, Colorado, USA.
- Sparks, R. E., J. C. Nelson, and Y. Yin. 1998. Naturalization of the flood regime in regulated rivers. *BioScience* **48**:706–720.
- Stohlgren, T. J., T. N. Chase, R. A. Pielke, Sr., T. G. F. Kittels, and J. S. Baron. 1998. Evidence that local land use practices influence regional climate, vegetation, and stream flow patterns in adjacent natural areas. *Global Change Biology* **4**:495–504.
- Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* **9**:45–64.
- Tabacchi, E., A. M. Planty-Tabacchi, M. J. Salinas, and H. Decamps. 1996. Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. *Regulated Rivers Research & Management* **12**:367–390.
- Tanner, J. E., T. P. Hughes, and J. H. Connell. 1994. Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology* **75**:2204–2219.
- Tanner, J. E., T. P. Hughes, and J. H. Connell. 1996. The role of history in community dynamics: a modelling approach. *Ecology* **77**:108–117.
- Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. Pages 301–304 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Tepedino, V. J. 1979. The importance of bees and other insect pollinators in maintaining floral species composition. Pages 39–150 in *The endangered species: a symposium*, 7–8 December 1978, Brigham Young University, Provo, Utah, USA. Great Basin Naturalist Members **3**.

- Terman, M. R. 1997. Natural links: naturalistic golf courses as wildlife habitat. *Landscape and Urban Planning* **38**:183–197.
- Thomson, J. D., R. C. Plowright, and G. R. Thaler. 1985. Matacil insecticide spraying, pollinator mortality, and plant fecundity in New Brunswick forests. *Canadian Journal of Botany* **63**:2056–2061.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:350–363.
- Turner, B. L., II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Matthews, and W. B. Meyer, editors. 1990. *The earth as transformed by human action: global and regional changes in the biosphere over the past 300 years*. Cambridge University Press, New York, New York, USA.
- Turner, B. L., II, and W. B. Meyer. 1994. Global land-use and land-cover change: an overview. Pages 3–10 in W. B. Meyer and B. L. Turner II, editors. *Changes in land use and land cover: a global perspective*. Cambridge University Press, Cambridge, UK.
- Turner, B. L., II, R. H. Moss, and D. L. Skole. 1993. Relating land use and global land-cover change: a proposal for an IGBP-HDP core project. HDP Report Number 5. International Geosphere–Biosphere Programme, Stockholm, Sweden.
- Turner, M. G., editor. 1987. *Landscape heterogeneity and disturbance*. Springer-Verlag, New York, New York, USA.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* **20**:171–197.
- Turner, M. G., and V. H. Dale. 1998. Comparing large, infrequent disturbances: What have we learned? *Ecosystems* **1**:493–496.
- Turner, M. G., V. H. Dale, and E. E. Everham, III. 1997a. Fires, hurricanes, and volcanoes: comparing large-scale disturbances. *BioScience* **47**:758–768.
- Turner, M. G., R. H. Gardner, and R. V. O'Neill. 1995. Ecological dynamics at broad scales. *BioScience* **45**:(Supplement)S29–S35.
- Turner, M. G., W. H. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* **5**:731–742.
- Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997b. Effects of patch size and fire pattern on early post-fire succession on the Yellowstone Plateau. *Ecological Monographs* **67**:411–433.
- Turner, M. G., D. N. Wear, and R. O. Flamm. 1996. Land ownership and land-cover change in the Southern Appalachian Highlands and the Olympic Peninsula. *Ecological Applications* **6**:1150–1172.
- Urban, D. L., R. V. O'Neill, and H. H. Shugart. 1987. Landscape ecology. *BioScience* **37**:119–127.
- U.S. Department of Agriculture Soil Conservation Service. 1992. 1992 summary report: natural resources inventory. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C., USA.
- U.S. Department of Commerce, Bureau of the Census. 1975. *Historical statistics of the United States, colonial times to 1970. Bicentennial edition. Parts 1 and 2*. U.S. Government Printing Office, Washington, D.C., USA.
- U.S. Department of Commerce, Bureau of the Census. 1977. *Statistical abstract of the United States: 1977 (98th edition)*. U.S. Government Printing Office, Washington, D.C., USA.
- U.S. Department of Commerce, Bureau of the Census. 1991. *Statistical abstract of the United States: 1991 (111th edition)*. U.S. Government Printing Office, Washington, D.C., USA.
- U.S. Department of Commerce, Bureau of the Census. 1996. *Statistical abstract of the United States: 1996 (116th edition)*. U.S. Government Printing Office, Washington, D.C., USA.
- Valone, T. J., and J. H. Brown. 1995. Effects of competition, colonization, and extinction on rodent species diversity. *Science* **267**:880–883.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494–504.
- von Hagen, B., S. Beebe, P. Schoonmaker, and E. Kellogg. 1998. Nonprofit organizations and watershed management. Pages 625–641 in R. J. Naiman and R. E. Bilby, editors. *River ecology and management*. Springer-Verlag, New York, New York, USA.
- Walker, L. R., and S. D. Smith. 1997. Impacts of invasive plants on community and ecosystem properties. Pages 69–86 in J. O. Luken and J. W. Thieret, editors. *Assessment and management of plant invasions*. Springer-Verlag, New York, New York, USA.
- Wallin, D. O., F. J. Swanson, and B. Marks. 1994. Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. *Ecological Applications* **4**:569–580.
- Warner, R. E. 1994. Agricultural land use and grassland habitat in Illinois: Future shock for Midwestern birds? *Conservation Biology* **8**:147–156.
- Warren, P. H., and M. Spencer. 1996. Community and food-web responses to the manipulation of energy input and disturbance in small ponds. *Oikos* **75**:407–418.
- Watson, R. T., M. C. Zinyowera, and R. Moss, editors. 1998. *The regional impacts of climate change: an assessment of vulnerability. A special report of the IPCC Working Group II*. Cambridge University Press, New York, New York, USA.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* **35**:1–22.
- Wear, D. N., M. G. Turner, and R. O. Flamm. 1996. Ecosystem management with multiple owners: landscape dynamics in a Southern Appalachian watershed. *Ecological Applications* **6**:1173–1188.
- Weller, D. E., T. E. Jordan, and D. L. Correll. 1998. Heuristic models for material discharge from landscapes with riparian buffers. *Ecological Applications* **8**:1156–1159.
- Wiens, J. A. 1996. Wildlife in patchy environments: metapopulations, mosaics, and management. Pages 53–84 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C., USA.
- Wilkie, D. S., and J. T. Finn. 1988. A spatial model of land use and forest regeneration in the Ituri Forest of north-eastern Zaire. *Ecological Modelling* **41**:307–323.
- Wilkinson, C. F., and H. M. Anderson. 1987. *Land and resource planning in the national forests*. Island Press, Washington, D.C., USA.
- Williams, M., editor. 1990. *Wetlands: a threatened landscape*. Basil Blackwell, Oxford, England.
- Wilson, C. J., R. S. Reid, N. L. Stanton, and B. D. Perry. 1997. Effects of land-use and tsetse fly control on bird species richness in southwestern Ethiopia. *Conservation Biology* **11**:435–447.
- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* **273**:1558–1561.
- WRI [World Resources Institute]. 1997. *World resources: 1996–1997*. World Resources Institute, Washington, D.C., USA.

- Yarie, J. K., L. Viereck, K. Van Cleve, and P. Adams. 1998. Flooding and ecosystem dynamics along the Tanana River. *BioScience* **48**:690–695.
- Zobel, D. B., L. F. Roth, and G. H. Hawk. 1985. Ecology, pathology, and management of Port Orford cedar (*Chamaecyparis lawsoniana*). General Technical Report PNW-184. U.S. Department of Agriculture, Forest Service, Portland, Oregon, USA.

SUPPLEMENTARY MATERIAL

A brochure for land managers and a one-hour video illustrating the concepts in the Report are available at cost (\$4.00 for the brochure; \$12.00 for the video) from The Sustainable Biosphere Initiative, Ecological Society of America, 1707 H Street, N.W., Suite 400, Washington, DC 20006 (e-mail: esaHQ@esa.org). A pdf version of the brochure is also posted on the ESA web site.

In addition, a set of PowerPoint slides illustrating the concepts discussed in this report is available in ESA's Electronic Data Archive: *Ecological Archives* A010-003.
