

Land Use

Land-use change in the United States represents an enormous uncontrolled experiment in the ways habitat changes influence plants and animals. When cities were built, land was plowed, or forests were cut, the effects on our native biota were not considered. Of course, humans have influenced the flora and fauna of North America over the ages. Native Americans established settlements, practiced agriculture, hunted, and used fire to induce vegetation changes (Denevan 1992). Land-use changes, however, have been particularly profound since Europeans settled North America three centuries ago. Landscapes have become mosaics of natural and human-influenced patches, and once-continuous natural habitats are becoming increasingly fragmented (for example, Burgess and Sharpe 1981; Harris 1984). Our nation's lands experienced tremendous changes in response to human activities, but our understanding of how land-use history affected the plants and animals in our modern landscapes is incomplete.

The term *land-use change* has several meanings; we use it to include changes in both land cover and land use. *Land cover* refers to the habitat or vegetation type present, such as forest, agriculture, and grassland. Land-cover change describes differences in the area occupied by cover types through time. Both losses and gains are included. For example, changes in how much forest occurs across a landscape may reflect additions as croplands or rangelands are abandoned and forests regrow. Forest cover may also be lost to harvest or to development. In addition to tracking the amount of cover types, land-cover change also describes shifts in the spacing of cover types across the landscape over time. For example, forest may occur in a large block, or it may exist as several smaller parcels. Land use is usually defined more strictly and refers to the way in which, and the purposes for which, humans employ the land and its resources (Meyer 1995). For example, a place that is in forest cover may be used for low-density housing, logging, or recreation. Land-use change encompasses all those ways in which human uses of the land have varied through time.

Land-use patterns have important influences on biological diversity—that is, the abundance, variety, and genetic constitution of native animals and plants—for several reasons. First, land-use activities may alter the relative abundances of natural habitats and result in the establishment of new land-cover types. The introduction of new cover types can increase the variety of species by providing a greater diversity of habitats. Natural habitats, though, are often reduced, leaving less area available for native species. Species that are not native to the locale may gain a foothold and out-compete the native species (see chapter on Nonindigenous Species). Second, the spatial pattern of habitats may be altered, often resulting in the fragmentation of once-continuous habitat. The effects of habitat fragmentation on animals, plants, and their habitats are numerous (see summaries by Saunders et al. 1991 and Noss and Csuti 1994), and the biological diversity of native species is almost always reduced. Third, land-use activities may change the natural pattern of environmental variation, especially by causing changes in natural disturbance patterns. For example, the environment may be changed directly when fire control and logging alter the frequency and extent of natural fires. Environmental scientists understand that natural disturbances create and maintain biological diversity by creating a mosaic of habitats (see chapter on Natural



Courtesy/Agricultural Services, USDA

Processes). In general, the chances of losing native animal and plant species and disrupting ecological functions increase when the patterns of natural habitats are altered.

The relation between land-use change and animal and plant communities sets the stage for understanding our present-day fauna and flora and for managing our lands. Both worldwide and in the United States, land cover today is altered principally by direct human use: agriculture, raising of livestock, forest harvesting, and construction (Meyer 1995). Our human society relies on natural habitats for a variety of services including productivity, recycling of nutrients, breakdown of wastes, and maintenance of clean air, water, and soil. The rate and quality of these services, and their capacities to recover from stress, often depend directly on communities of native plants and animals (Schulze and Mooney 1993; Tilman and Downing 1994; Mooney 1996). The ways in which plants and animals respond to new kinds of human-caused environmental disturbances can help us learn more about the tolerances of species and their needs. We present a historical perspective on land-use change and its effects on biological diversity in the United States and consider what this may teach us and what to anticipate from current land-use trends.

Historical Perspective on Land Use and Biological Diversity

The vegetation in our nation's landscapes is the result of a combination of environmental characteristics (such as soils, climate, and topography) and land-use history (Foster 1992; White and Mladenoff 1994; Meyer 1995). At the time of European settlement, forests covered about half the present lower 48 states. Most of the forestland was in the more moist East and Northwest regions, and it had already been

Fig. 1. National trends in the amount of land in different uses for the contiguous United States since the mid-1800's. Data obtained from Powell et al. (1993) and Fedkiw (1989). The amount of forest in 1630 was about 423 million hectares (Powell et al. 1993), and the amount of cropland in 1800 was probably less than 8.1 million hectares (Fedkiw 1989).

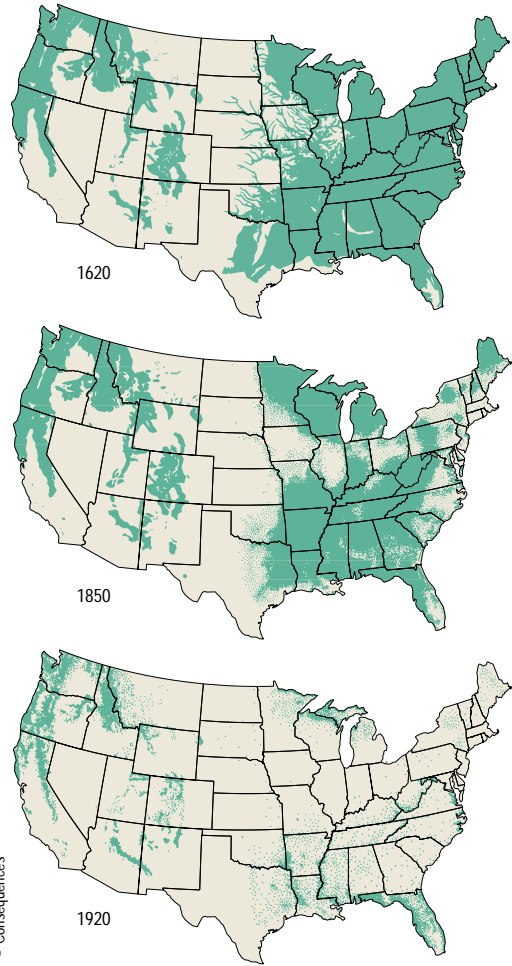
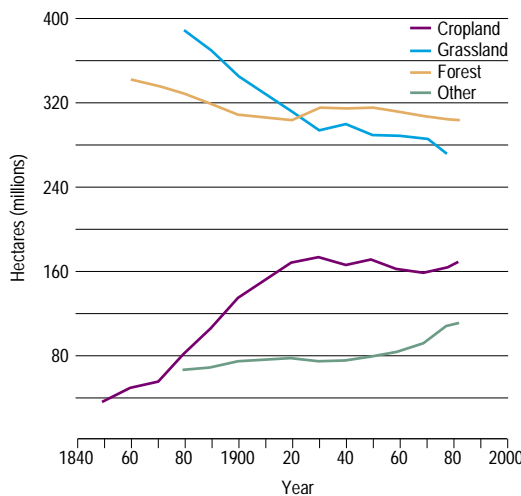


Fig. 2. Approximate area of virgin old-growth forest in the contiguous United States in 1620, 1850, and 1920. Note that this does not depict total forest area because forests that have regrown after clearing are not shown (from Meyer 1995).

altered by Native American land-use practices (Williams 1989). Clearing of forests for fuel, timber, and other wood products and opening the land for crops led to a widespread loss of forest cover that lasted through the early 1900's (Fig. 1). So extensive was this loss that by 1920 the area of virgin forest remaining in the contiguous United States was only a tiny fraction of that present in 1620 (Fig. 2).

Cropland increased at the expense of other land covers throughout much of American history (Meyer 1995). Cropland reached a peak in the 1930's and has since fluctuated around 162 million hectares (Fig. 1). Irrigated cropland became significant only in the late 1800's, and it increased rapidly after 1945, primarily in the drier West, with the advent of more advanced technologies like center pivot irrigation. By 1980, about one-eighth of all cropland was irrigated. While dry cropland was being irrigated, however, wetlands were being drained for agriculture. Between the 1780's and 1980's, 53% of American wetlands were converted to other

uses (Meyer 1995). Between the 1950's and 1970's alone, nearly 4.5 million hectares were lost. Grasslands also experienced a net decline (Fig. 1).

Developed land in the United States has expanded as the population has grown. Most of the population of the United States now lives in cities, towns, and suburbs rather than on farms. Americans spread out across the land as transportation technologies improved, especially as the automobile became the primary mode of transportation. Present-day patterns of settlement involve more land per person than in the past, and homes and subdivisions are more dispersed across the landscape. A frontier of rapid and sometimes chaotic land-use change surrounds urban areas (Meyer 1995). Trends in developed land are unique because they run in only one direction—that is, developed land expands and does not revert to other categories. Thus, the distribution of developed land across our nation will leave a long-lasting footprint on our landscapes.

Ninety-seven percent of the nation's surface area is land, and consequently most of the water that enters streams and lakes is affected by activities on land (National Research Council 1992). Declines in stream and river conditions in the United States are well documented (Naiman et al. 1995). Of the 1 billion hectares

of land in the contiguous United States, nearly half have been cultivated or grazed by livestock (Bureau of the Census 1990). Changes in drainage and erosion that accompany agriculture have substantial effects on fresh waters (National Research Council 1992). Urban areas account for only 3% of the land in the United States, but the effects of densely settled areas on our water resources are extreme. As cities are built, natural wetlands and floodplains are replaced with surfaces such as asphalt, cement, and buildings that cannot absorb water. Flash flooding becomes common, and additions of waste and pollutants to downstream waters increase (National Research Council 1992). Thus, land-use change affects not only the land but also the waters.

Regional Variation in Historical Land-Use Change

The timing and sequence of land-use changes in the United States have varied among regions. Territories of the United States were acquired from east to west as land was purchased and treaties were signed (Fig. 3). Settlement patterns also followed this trend as new lands were acquired by an expanding nation and people were encouraged to move

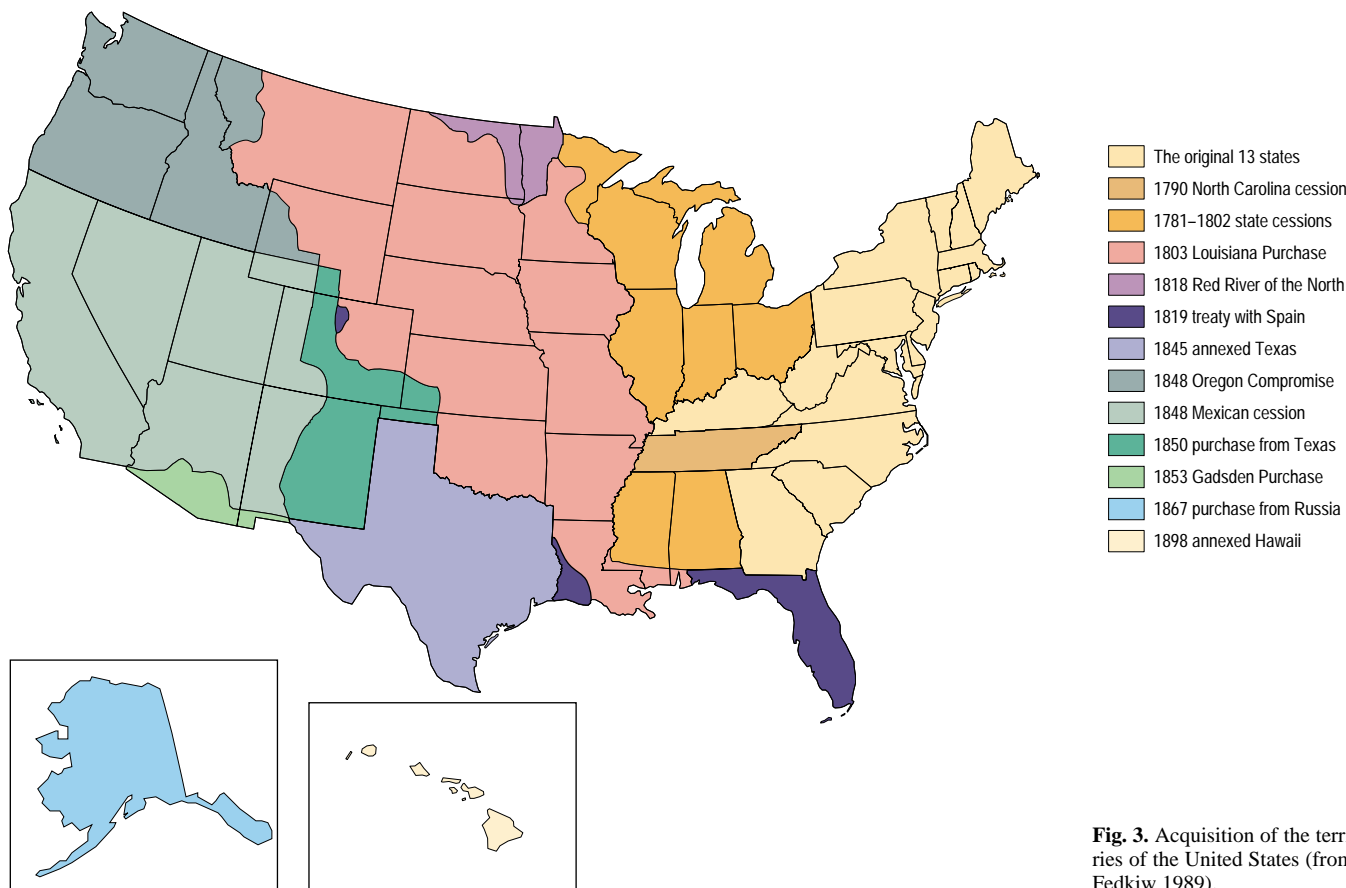


Fig. 3. Acquisition of the territories of the United States (from Fedkiw 1989).

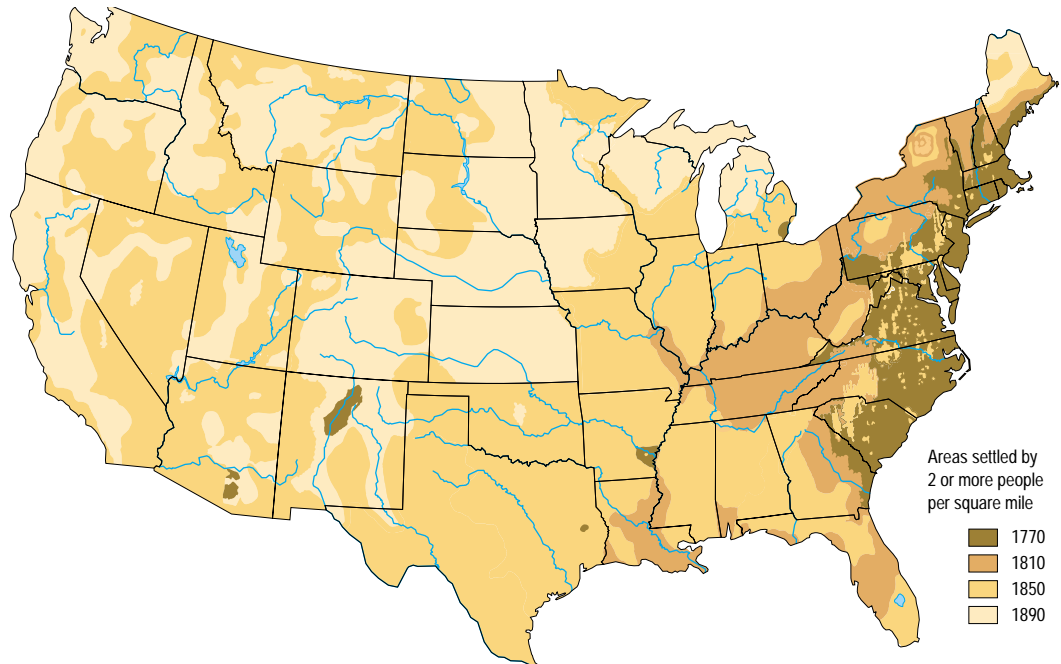


Fig. 4. The progress of settlement of the contiguous United States from 1770 to 1890. The Eastern Seaboard was settled first, but westward movement was rapid (from Fedkiw 1989).

westward (Fig. 4). Clearing of forests rapidly followed settlement, beginning in the East and proceeding westward. Some originally cleared areas—such as New England, the Southeast, and the upper Midwest—have now become reforested because of lack of cultivation (Fig. 5). In other regions, clearing for agriculture has been more permanent (for example, the lower Midwest), or harvest of virgin forest has continued until recent times (Pacific Northwest). In this section, regional patterns of land-use change are compared to illustrate the diversity of changes across the country.

Fig. 5. Postsettlement changes in forest cover for several regions of the United States. Initial deforestation occurred in the Northeast (for example, Petersham Township, Massachusetts [Foster 1992]), with the South (for example, the Georgia Piedmont [Johnson and Sharpe 1976]) and Midwest (for example, Cadiz Township, Wisconsin [Dunn et al. 1991]) following later.

Deforestation and Reforestation in the Eastern United States

The eastern United States has undergone dramatic changes in the area covered by forest during the past 250 years. Foster's (1992) analysis of land-use change in Petersham Township, central Massachusetts, illustrates the cycle of forest clearing and regrowth that was typical of much of the Northeast. Forest clearing by European settlers began around 1730 and

proceeded at a pace of 1%–4% of the original forest per year. Open land covered half of Petersham Township in 1800, and nearly 85% of the land was open by 1850 (Figs. 5 and 6). Remaining uncleared forests generally occurred in less accessible locations, such as steep slopes, but were still used for grazing, timber, and fuelwood. Farming became unprofitable and farm abandonment commenced in the mid-1800's; thereafter, forests gradually grew back on neglected fields. This process led to the broad-scale establishment of forest cover over the entire region. Most recently (1920–1990), Petersham Township is characterized by residential development and almost no agriculture.

The patterns described by Foster (1992) were generally repeated throughout the northeastern United States. Ninety-five percent of Dutchess County, New York, was in farmland as late as 1880, but farming had declined dramatically by the 1930's (Glitzenstein et al. 1990). Indeed, much of New York State followed a similar pattern (Hill 1985; Nyland et al. 1986; Smith et al. 1993). Forest regrowth, however, was not always the rule. Forest cover in Franklin Township, New Jersey, increased between 1880 and 1943 but then declined; only 16% of the area was forested in 1986 (White et al. 1990).

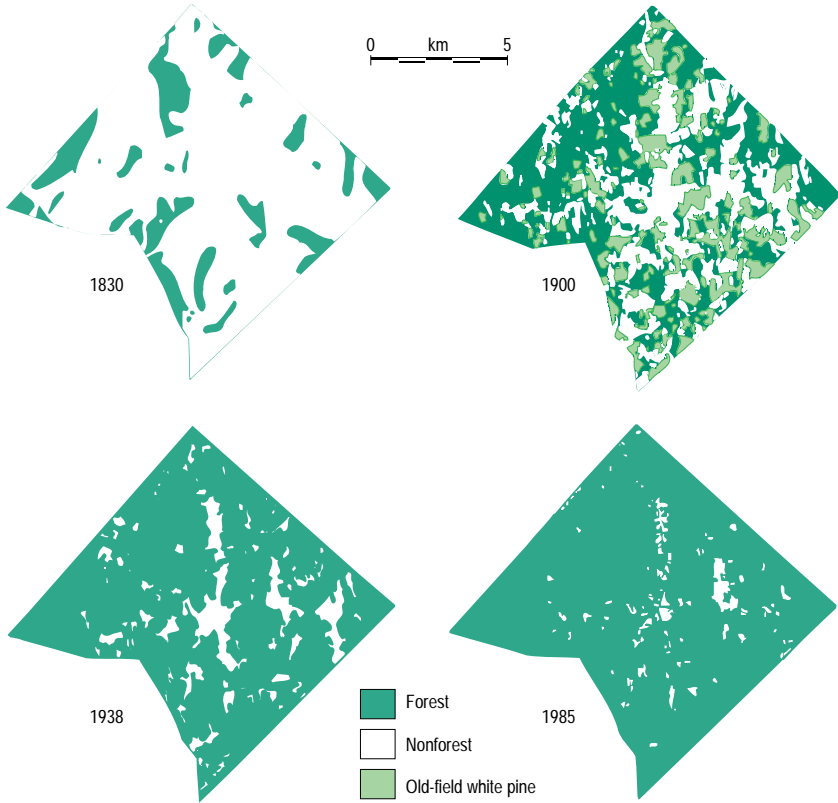
The Southeast underwent a similar cycle of forest clearing and regrowth that occurred about 50 years later than in the Northeast (Turner 1987; Fig. 5). For example, before European settlement the vegetation of Georgia was primarily forest, although it had been modified for centuries by Native Americans (Stewart 1956). Following European settlement, Coastal Plain

forests were cut between 1866 and 1890, and stands of virgin pine were completely cut by 1895. Indeed, only 2% of the original longleaf pine forest that covered much of the Coastal Plain remains throughout the Southeast (Noss 1989). Upland broadleaf forests were cleared continuously for farming during the 1800's, and by 1930, more than 80% of the Piedmont had been cleared at least once. A great many farms were abandoned following the boll weevil infestation of cotton during the early 1900's. Most of the abandoned farms reverted through succession to pine (primarily loblolly pine and shortleaf pine), and some of the Piedmont pine forests are now making the transition to broadleaf forest (Turner 1990).

Deforestation of the Midwest

The oak-hickory forests that range from the Ozark Mountains to the Appalachian Mountains owe their current condition largely to human activity, which began with Native American activity before 1600 (DeVivo 1990; Denevan 1992). Native peoples used fire to move game animals, to open up the forest, and to clear underlying brush and saplings. The native peoples also cleared land for agriculture in river valleys and on flat, moist upland sites (Parker 1991). Their use of fire and forest clearing affected the types of trees found in the forest communities, so that the widespread dominance of oak and hickory most likely had its origin in Native American practices.

The European settlers who began to arrive in the Midwest in the late 1700's initially adopted Native American methods of clearing forests. Much of the land cleared in the early 1800's was abandoned as soil fertility declined and settlers moved farther west. But as technology developed by the mid-1800's, forests were permanently cleared. In Illinois, for example, only 31% of the forest area present in 1820 exists today (Iverson 1991; Fig. 7). Until 1860 forests were the sole source of potential cropland, and by 1860 the timber industry was thriving in Illinois. Iverson (1991) makes a striking comparison of deforestation rates in Illinois from 1820 to 1923 and recent rates of forest clearing in three tropical countries (Table 1). It is instructive to note that deforestation in the United States was of a similar magnitude as present-day deforestation rates in the tropics.



Overhunting and fragmentation of the mid-western forest into smaller pieces caused the disappearance of many wide-ranging mammals by 1860 (for example, black bear, gray wolf, mountain lion), and even the white-tailed deer was eliminated from some areas by 1900 (Reeves 1976), but most plant and animal species were able to persist in habitat fragments. Clearing and widespread grazing continued until the late 1930's, but since that time continued disturbance of the land has been greatly reduced (Parker 1991). Land used for grazing in the central Midwest has decreased from 70% in the 1930's to around 30% today. Reforestation has occurred on the hilly portions in the south and west of the region, while intensive agriculture is still practiced in the relatively flat northern areas.

The central hardwood forest ecosystem of the Midwest is diverse and resilient. The region apparently has survived massive human disturbance with the disappearance of few native species. Some species are rare because their

Fig. 6. Spatial pattern of forest-cover changes reconstructed for Petersham Township, Massachusetts (by Foster 1992). Small isolated patches of forest were present in 1830, but by 1985, secondary succession had resulted in extensive connected forest cover.

Location	Land cover	From (year)	Area (hectares)	To (year)	Area (hectares)	Percent cleared per year
Rondonia, 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, U.S.	Forest	1820	55,870	1870	24,290	1.13
	Forest	1870	24,290	1923	90	0.87
Illinois, U.S.	Prairie	1830	87,550	1860	10	3.33

Table 1. Comparison of recent deforestation rates in the tropics with conversion of forest and prairie in Illinois during the settlement period as presented by Iverson (1991).

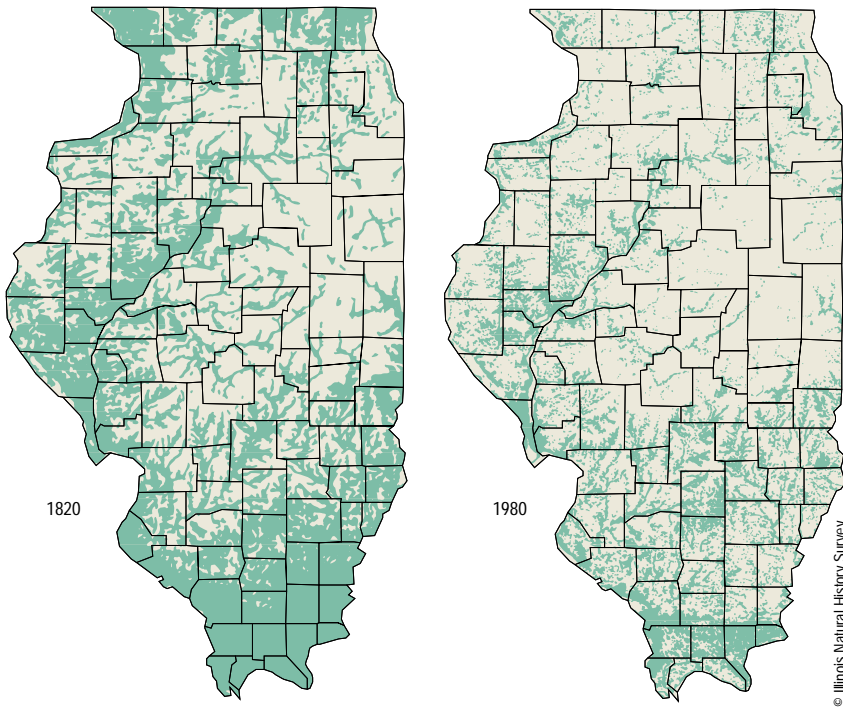


Fig. 7. The distribution of forest cover in Illinois in 1820 and 1980. Most remaining forests in Illinois occur within 300 meters of rivers and streams (from Iverson 1991).

habitat has declined or because they were harvested by humans. Many other species are rare because of a reduction in environmental patchiness (see chapter on Natural Processes) due to natural disturbances such as periodic fires and storms (Anderson and Schwegman 1991).

The Plains and the Loss of Native Prairie

Along the boundary between forests and prairies, it was the forested lands that were first settled. Settlers believed that the prairie was unsuitable for settlement because of lack of wood and drinking water, lack of protection from winter storms, and the lack of trees, which was thought to be caused by infertile soils (Latta 1938; Anderson 1970). Settlement began in the early 1800's, but even as late as 1836 only small prairies near woodlands were settled, despite the invention of plows capable of tilling the thick prairie sod and the high crop yields obtained from prairie soils (Anderson 1970). After the railroads were established in the 1850's and 1860's, crops and supplies could be transported economically, and the prairies were then rapidly settled (Barrows 1910; Anderson 1970).

Before 1800, Illinois was nearly two-thirds prairie grassland and one-third forest, but by 1850 prairie habitat was reduced by 75% (Graber and Graber 1963). Although natural prairie became extremely rare by 1920, diversified commercial farming that included rotation farming and livestock production allowed grasslands to remain common between 1900 and 1950, and many prairie vertebrates thrived

(Warner 1994). The development of high-yield mechanical and chemical cultivation practices led to intensive row cropping by the 1960's, and grassland habitats declined sharply (Warner 1994). Only about 0.01% of the original unplowed prairie now remains (Iverson 1988), which has led to significant changes in the abundance of prairie birds between 1850 and the present (Table 2), with some bird species increasing and others declining.

Cattle raising was largely a frontier activity, and by 1865 the cattle industry had moved to Illinois, Iowa, and Missouri and was pushing farther west. Spanish cattlemen introduced herds to both Texas and California before 1865 (Rasmussen 1974). Herds of cows roamed freely on the plains with little tending and by the 1880's had expanded throughout the northern plains (Fedkiw 1989). After World War I, ranch farming became more common because it reduced some of the economic hazards of herding. Cattle numbers on the plains have varied widely in this century because of unpredictable markets and weather. Range conditions were probably at their worst in the late 1920's.

The decline in grasslands (Fig. 1) was primarily due to a shift to cropping, mostly wheat. Beginning in the 1880's, dryland farming and irrigation development in the semiarid West were encouraged by the government and by the railroad companies. By 1920 more than 75 million hectares had been added to annual cropland, mostly west of the Mississippi (Fedkiw 1989). Today, very little of the original extensive native prairies remains.

Pacific Northwest Forests

Cutting of forests in the Pacific Northwest began in the 1800's when European settlers arrived in the region. The extensive forests covering the lowlands and river valleys were viewed as blocks to progress and were systematically burned and cleared for agriculture (Forest Ecosystem Management Assessment Team 1993). In the late 1800's and early 1900's, commercial logging began to increase on the uplands but did not begin in earnest on federal lands until after World War II. European methods of forest management were gradually adopted on most federal and private lands—techniques such as clear-cutting, removal of logs and snags, slash burning, thinning, and planting stands of a single species. The assumption was that forests managed in this manner could be cut and regrown at relatively short intervals (for example, 40–80 years) without negatively affecting water quality, fish, soils, or land animals. Stream and riparian ecosystems in the region first suffered damage from grazing and mining that occurred from the 1860's to 1910, and then from the logging, roads, fire

Species	Before 1900 ^a	1906–1909 ^b		1956–1958 ^c		1987–1989 ^d		USFWS ^e Percent change
		Percent	Rank	Percent	Rank	Percent	Rank	
Eastern meadowlark ^f	Abundant	25.5	2	20.0	2	11.8	2	-67.0
Dickcissel	Abundant	13.1	3	8.7	4	7.7	5	-46.7
Grasshopper sparrow	Abundant	5.9	5	5.3	6	8.6	4	-56.0
Bobolink	Abundant	25.8	1	9.7	3	11.4	3	-90.4
Henslow's sparrow	Abundant	<1.0	15	<1.0	14	1.6	12	*9
Red-winged blackbird	Very common	9.9	4	36.2	1	26.8	1	-18.8
Greater prairie-chicken	Very common	<1.0	13	0.0	16	0.0	16	*9
Upland sandpiper	Very common	2.3	9	<1.0	12	<1.0	13	-16.8
Vesper sparrow	Common	1.3	11	1.4	10	<1.0	15	+12.1
Horned lark	Common	4.9	6	4.8	7	<1.0	14	0.0
Field sparrow	Common	4.0	7	2.9	9	5.6	7	-52.6
Song sparrow	Common	2.6	8	1.0	11	3.3	10	-29.3
Savannah sparrow	Common	2.3	10	5.8	5	3.5	9	-58.9
American goldfinch	Common	1.2	12	3.1	8	4.7	8	-42.8
Common yellowthroat	Common	<1.0	14	<1.0	15	5.8	6	-8.8
Sedge wren	Common	<1.0	16	<1.0	13	2.8	11	-22.5

^a Relative abundance before 1900 based on the works of Nelson (1876) and Ridgway (1873, 1889, 1895).

^b Relative abundance 1906–1909 based on censuses of Gross and Ray from about 380 hectares of ungrazed grass, mixed-hay, and pasture in northern and central Illinois (Forbes 1913; Forbes and Gross 1922).

^c Relative abundance 1956–1958 based on censuses of Graber and Graber (1963) from approximately 290 hectares of ungrazed grass, mixed-hay, and pasture in northern and central Illinois.

^d Relative abundance from present study (1987–1989) based on censuses of about 400 hectares of ungrazed prairie and agricultural grasslands in northeastern and east-central Illinois.

^e Estimated population change within Illinois between 1967 and 1989 based on the U.S. Fish and Wildlife Service's Breeding Bird Survey (U.S. Fish and Wildlife Service, unpublished data).

^f For 1906–1909 and 1956–1958, relative abundance estimates are for eastern and western meadowlarks combined.

^g Present on too few routes for accurate trend analysis.

Table 2. Relative abundance of prairie birds within Illinois, 1850 to 1989 (from Herkert 1991).

management, and irrigation that occurred in the twentieth century (Wissmar et al. 1994).

As a result of more than a century of logging and fire control, the forests of the Pacific Northwest presently consist of a highly fragmented mosaic of clear-cuts, thinned stands, and young (and often single species) plantations interspersed with uncut natural stands. In addition, the development of extensive road systems to access the forests has further modified the landscape. The road density often equals or exceeds the density of natural stream channels in the basin—more than 2.5 kilometers of road per square kilometer. Only about 15% of the 10 million hectares dominated by Douglas-fir remains as ancient forests in the 12 national forests studied by Morrison et al. (1991); the percentage appears to be less on private and state lands. The remaining ancient forest, for the most part, occurs in highly fragmented stands and is subjected to greater damage from windstorms and human intrusions caused by edge effects and the extensive road system. Many of the remaining stands are in small patches (less than 30 hectares) and within 125 meters of roads or clear-cuts, significantly decreasing their value as habitat for native plants and animals.

The Olympic Peninsula in Washington state provides a regional illustration of the changes that have taken place throughout the Pacific Northwest (Fig. 8). Since 1940 nearly 76% of the Olympic Peninsula's ancient forests have been logged (Fig. 8a). In 1940, 87% of the ancient forest was in patches greater than 4,000 hectares, whereas by 1988, the forest was so

fragmented that 60% of the ancient forest occurred in patches of fewer than 40 hectares (Fig. 8b). In addition, very little of the low-elevation forest remains today. In the Pacific Northwest, many species are only found below elevations of 1,200 meters and others are only found below 600 meters. Most of this species-rich lowland forest occurs in small stands or fragmented webs with the natural communities endangered by their proximity to forest edge (Fig. 8c).

The West and Southwest

In the late 1870's, following serious efforts by European immigrants to subdue the Native Americans, much of the Southwest was opened to settlement (Cooper 1960). The history of settlement and vegetation change of southwestern pine forests since settlement has been documented by Cooper (1960). Early accounts of these forests stressed the open nature of the woods, luxurious grass swards, and lack of gullying. It is likely that the open nature of the forest was maintained, in part, by use of fire by Native Americans. Some tribes, such as the Navajo, also maintained extensive herds of stock. The introduction and subsequent mismanagement of livestock in the West, however, produced profound changes in plant cover (Cooper 1960). Deterioration of watershed condition was rapid following settlement, reaching its worst state by the turn of the century and leading to serious concern over water supply. The adverse ecological effects of overgrazing are well known (for example, see West 1993).

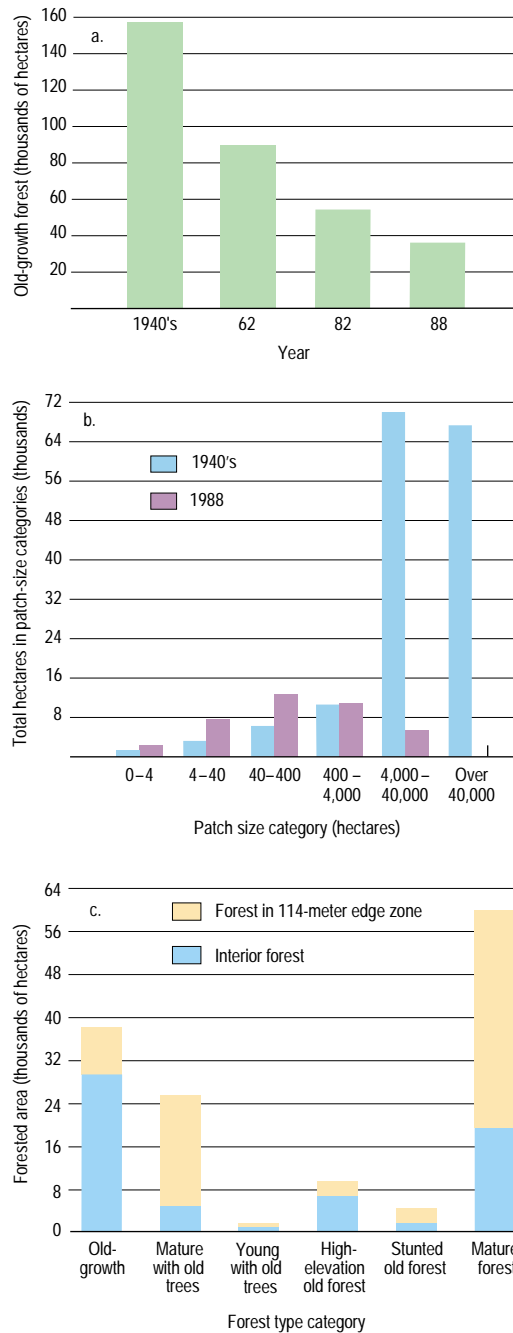


Fig. 8. Recent historical changes in abundance and landscape structure of old-growth forest on the Olympic Peninsula, Washington (from Morrison et al. 1991): a) area of old-growth forest through time; b) frequency distribution of old-growth by patch size in the 1940's and 1988 indicates the dramatic shift from large contiguous old-growth forest to small isolated tracts; and c) area of different forest types considered interior forest (more than 114 meters from a patch edge) and occurring within the edge zone (less than 114 meters from a patch edge) in 1988 illustrates that a considerable proportion of the present forest is subject to edge effects.

In the northern Rocky Mountains, the post-1860 rush of miners greatly accelerated land-use change. Madison Valley, Montana, offers a good example of settlement patterns (Wyckoff and Hansen 1991). Although Native Americans had migrated through the area, they had not maintained permanent settlements in the valley. Permanent settlement of the region by European immigrants began around 1870; these settlers introduced large numbers of livestock to the land, resulting in deleterious effects on many habitats. As range conditions deteriorated, fescue and wheatgrasses declined and were replaced by rabbitbrush, grama grasses, and sagebrush. Seasonal overgrazing by livestock caused particular damage to sensitive riparian and subalpine habitats (Wyckoff and Hansen 1991).

Recent land-use changes in the West are dominated by increased demand for housing development. In California, for example, the human population increased 25% between 1980 and 1990, leading to urbanization of 123,000 hectares of previously undeveloped land (Charbonneau and Kondolf 1993). Smaller cities in the Rocky Mountain states are also experiencing intense developmental pressure. Residential development is occurring nearer and nearer to large private and public landholdings; this geographic proximity makes forest and wildland management problematic. For example, management of natural fire becomes more of an issue when homes and businesses are nearby. In addition, dispersed residential development leads to extensive natural habitats becoming increasingly fragmented at fine scales. The sizes and connectivity of native habitats become reduced, making wildlife management more difficult.

Land-Use Change and Trends in Biological Diversity

The composition of plant and animal communities across the United States has undoubtedly changed continuously over the past 400 years as human uses of the land have changed. When Europeans arrived in North America, there were approximately 1.9 million people occupying the vast continent (Ubelaker 1988 in MacLeish 1994). The level of human activity on the land diminished rapidly in the sixteenth century as the large Native American populations dwindled following the introduction of European diseases (Denevan 1992). Human activity then increased rapidly as Europeans settled the landscape in the seventeenth and eighteenth centuries (Whitney 1994).

A clear picture of changes in biological diversity since European settlement is very difficult to obtain. Existing information suggests

Table 3. Loss of native vascular plant species for selected states (from Whitney 1994).

State	Number of native species	Native species extirpated or extinct	
		Number	Percent
Maine	1,500	84	5.6
Massachusetts	1,700	53	3.1
New York	2,000	59	3.0
Pennsylvania	2,100	62	3.0
Illinois	2,000	50	2.5
Indiana	1,900	22	1.2
Iowa	1,350	49	3.6
Ohio	1,800	84	4.7
Wisconsin	1,700–1,800	13	0.7

that many states have lost between 1% and nearly 6% of their flora (Table 3) and between 2% and 20% of their fauna (Table 4). Many of the plants that were lost were growing at the edges of their ranges. Others that were lost were associated with habitats that are now rare—like Coastal Plain wetlands and grasslands—or habitats that were associated with fire (Whitney 1994). Although many species were lost from portions of their ranges, relatively few have become extinct. Many species that are still present, though, have undergone dramatic changes in abundance.

State or region	Number of native species having bred in region ^a	Native species extirpated or extinct	
		Number	Percent
Mammals			
New England	70	6	9
Massachusetts	58	8	14
Pennsylvania	70	8	11
Ohio	65	13	20
Indiana	65	13	20
Illinois	67	8	12
Iowa	68	10	15
Missouri	70	3	4
Michigan	66	6	9
Minnesota	78	5	6
Birds			
Massachusetts	186	3	2
Pennsylvania	180 ^a	8	4
Ohio	188 ^a	8	4
Indiana	180 ^a	15	8
Illinois	215 ^a	16	7
Iowa	160 ^a	15	9
Missouri	184	32	17
Michigan	214 ^a	5	2
Minnesota	245 ^a	8	3
Wisconsin	220 ^a	4	2
Fish			
Connecticut	40	1	2
Massachusetts	41	1	2
Pennsylvania	180	28	15
Ohio	154	9	6
Indiana	168	10	6
Illinois	186	10	6
Iowa	140 ^a	12	9
Wisconsin	155	9	6

^a Approximate number.

Table 4. Summary of losses of native vertebrates for selected states (from Whitney 1994).

Effects of Fire Suppression on Ecosystems and Diversity

Fire suppression has been one of the great success stories of wildland management organizations. Over the last 100 years or so, public fire-fighting agencies such as the U.S. Forest Service, the Bureau of Land Management, the Bureau of Indian Affairs, and the National Park Service have developed an impressive array of fire-fighting technologies that have remarkably reduced acreage burned by wildfires (Pyne 1982).

In California, fires ignited naturally and by Native Americans before European settlement burned as much as 13% of the state in any one year (Martin and Sapsis 1992). With effective fire suppression beginning in the early twentieth century, burned acreage plummeted to 15% of presuppression values. Since 1970, however, suppression efforts have become less effective. California, for example, has experienced a doubling in acreage burned by wildfires, while the number of wildfires in the state has increased only slightly (Martin and Sapsis 1992). Other western states have also seen sharp increases in burned acreage. In recent years, fires that burned tens and hundreds of thousands of acres have occurred in California, Idaho, Montana, Oregon,

Washington, and Wyoming (Martin and Sapsis 1992; Agee 1993; Covington et al. 1994; Johnson et al. 1994). While most ecosystems occasionally experience very large fires (Romme and Despain 1989), the present-day frequency of such large fires appears unprecedented.

Ecosystems respond differently to fire suppression. Ecosystems that tend to be particularly cool and moist, such as certain boreal and subalpine ecosystems, burn so infrequently that the interval between fires is longer than the 75–100 years of effective fire suppression. Ecosystems that are extremely dry, such as deserts or cold, dry alpine ecosystems, are so unproductive that they accumulate fuel too slowly to have been affected by fire suppression (Martin 1982). Temperate ecosystems, where frequent, low-intensity wildfires had occurred in the past, are more likely to have been adversely affected by fire suppression (Agee 1993).

In these temperate, productive ecosystems, average fire size and severity have increased dramatically. Decades of fire suppression have left a legacy of increased fuel loads and ecosystems choked with an

understory of shade-tolerant, late-successional plant species (Figs. 1 and 2). These structurally homogeneous ecosystems are conducive to the large, severe fires, especially during hot, dry, windy periods in late summer or early fall. Such ecosystems have fewer structural breaks to retard fire spread and intensity, and their increased accumulations of live and dead fuels may burn longer and more completely. Plant and animal mortality in these ecosystems is relatively high following the large stand-replacing fires that are now much more likely to occur in these ecosystems.

Ecosystem recovery following stand-replacing fires potentially follows four stand-development stages: stand initiation, stem exclusion, understory reinitiation, and old-growth (Oliver 1981; Larson 1990; Oliver and Larson 1990; Fig. 3). Stand initiation is a period in which a site is reoccupied by an influx of colonizing species combined with a diverse mix of late successional species. During stem exclusion, competition induces self-thinning of weakened plants, leading to a marked decline in species richness and structural diversity. Forest canopies close, leaving understory species with



Fig. 1. Effects of fire exclusion in a Douglas-fir forest of western Montana 1909, 1928, 1938, and 1948 (from Gruell et al. 1982).

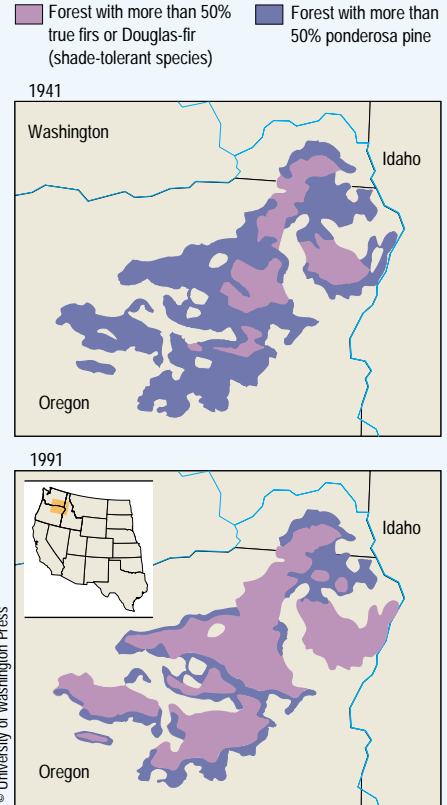


Fig. 2. Forest composition differences between 1941 and 1991 in the Blue Mountains of Oregon and Washington. Douglas-fir and true fir abundance have increased with fire suppression (from Langston 1995).

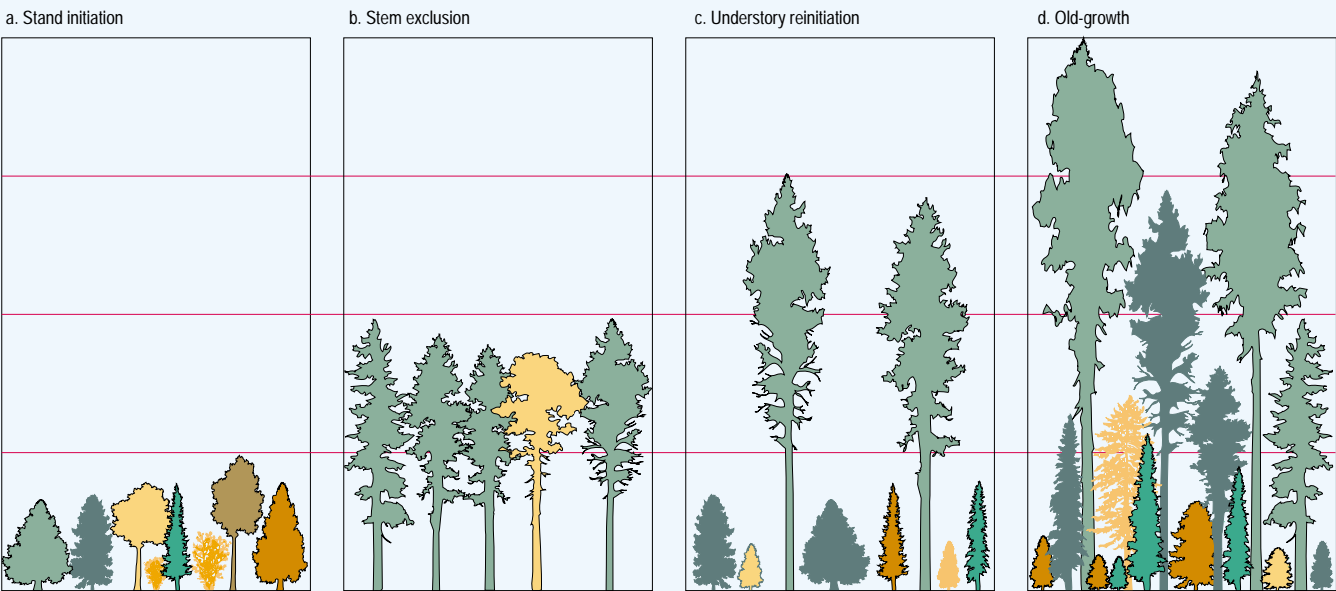


Fig. 3. Hypothetical stand development sequence. Note that all the species are present during a) stand initiation, a period of high species richness. Which species colonize following a disturbance depends strongly on which species were present, even in tiny populations, before the disturbance. Species richness drops during the intense competition of the b) stem exclusion stage, then increases again as succession proceeds toward c) understory reinitiation, and d) old-growth. Note the structural diversity as well as species richness in the old-growth stage. The timing of these stages following disturbance varies considerably with the ecosystem; the old-growth stage may be reached in 200 years or as long as 1,000 years.

inadequate light. Understory reinitiation begins once larger trees die, leaving holes in the canopy large enough for light to reach the forest floor, where late-successional, shade-tolerant species can grow and survive. Over time, an old-growthlike forest develops with characteristic multiple-age classes of trees and multiple canopy layers. Plant species richness peaks during the stand initiation stage, declines during stem exclusion, then slowly increases as growing space is provided by individual tree mortality and the reestablishment of an understory (Schoonmaker and McKee 1988; Stuart et al. 1993). In contrast, structural diversity peaks during old-growth, allowing for a greater richness of epiphytes and invertebrates (Schowalter 1989).

Before fire suppression, ecosystems accustomed to frequent, low-severity wildfires supported diverse landscapes composed of a variety of plant communities and successional stages. The resulting landscape mosaic typically burned irregularly. Some landscape patches had light, discontinuous fuel and burned cool and quickly; others had heavy, continuous fuel and burned hot and slowly or did not have enough available fuel to burn at all. Recovery from fire was equally varied. Patches that burned hot resembled small stand-replacing fires with stand development patches dominated by shade-intolerant species. In contrast, few to no overstory trees were killed and only some of the understory plants were killed in cool-burning patches. Shade-tolerant species reestablished themselves in the understory. Stands harboring complements of both early and

late successional species represented islands of high biological diversity.

The greatest effect of fire suppression on biological diversity is not on the diversity within a particular habitat (Whittaker 1977), but on the diversity of habitats across a landscape. Landscapes with high diversity resulting from fire perpetuate high species diversity by providing opportunities for the establishment and maintenance of early successional species and communities (Connell 1978; Reice 1994). Fire suppression, on the other hand, increases uniformity in habitats as competition eliminates early successional species, leaving only shade-tolerant understory plants to reproduce. For example, in the Klamath Mountains of northern California, recently burned landscapes had more (46–48) distinct habitat types that were more evenly distributed than equal-sized unburned areas (31) (Fox et al. 1992). Burned landscapes included habitat types dominated by early successional pines, shrubs, or herbaceous species, whereas unburned landscapes were more uniform in their cover of later successional fir-dominated communities.

Fire suppression has helped change the ecosystem dynamics of communities adapted to frequent, low-intensity wildfire. Complex landscapes are made simpler, some early and midsuccessional plants and animals are extirpated, shade-tolerant tree populations rapidly expand, and the relative importance of fire as a disturbance agent is reduced, while the importance of insects and pathogens is elevated (Covington et al. 1994). During droughts, for example,

excessively dense forests become further stressed, enabling pathogens and insects to reach high population levels (Johnson et al. 1994). Trees killed by drought, insects, or pathogens create abundant fuel that exacerbates fire hazard. When fire occurs in such a system, it is often larger and more severe than one expected in areas with a natural fire regime. Such a scenario is being played out in the forests in the Blue Mountains of eastern Oregon and southwestern Washington (Langston 1995).

Re-creating the natural fire regimes of ecosystems adapted to frequent, low-severity fire seems an obvious management choice if we want to enhance biological diversity and reduce the risk of catastrophic wildfire. Paradoxically, while fires help maintain native biological diversity, they also create opportunities for invasive alien species to become established. In many cases, these species are superior competitors, predators, or parasites on our native flora and fauna (Hobbs and Huenneke 1992) and could actually reduce native biological diversity. Thus, restoring a more natural fire regime will have to be carefully considered to maximize ecosystem benefits while minimizing biological and social costs.

See end of chapter for references

Author

John D. Stuart
Humboldt State University
Department of Forestry
Arcata, California 95521

In hindsight, the overall changes in many animal species proceeded in a predictable way. The large animals, especially predators such as wolves and mountain lions, disappeared soon after settlement. Numbers of furbearers diminished as they were trapped for their pelts. As forests were opened and prairies were plowed, forest edge and pioneering species replaced the forest-interior and grassland-interior species. Overharvesting and changes to freshwater habitats led to losses of many fishes.

Although these general trends are conspicuous, remarkably few studies have addressed the changes in species abundance or composition associated with land-use change since Europeans came to America. The kinds and proportions of trees in forests can sometimes be reconstructed from historical records such as General Land Office surveys and compared with the makeup of present-day forests. Although past land use can be compiled from deed and tax documents, there is little

numerical information on the abundance and distribution of most nonwoody plants and most animals. Birds are the best-studied animals, yet most information on them does not extend back farther than the 1950's.

Composition of Forest Communities, Then and Now

Are present-day forests similar in composition to the forests encountered by the early settlers? Dramatic changes in forest cover have occurred throughout the eastern United States and upper Midwest during the past two centuries, suggesting that our forests displayed considerable resilience—that is, the ability to recover from disturbance. On a regional basis, the distribution of forest types closely resembles the presettlement patterns, but on closer inspection, there are substantial differences in present-day forests.

In the 1700's in Petersham Township, Massachusetts, regional forest communities

were distributed along slopes and valleys much as they are today (Foster 1992). Trees such as birch, red maple, and oaks, which are found in young forests or which can resprout, have increased in number, however. At the same time, there has been a decline in long-lived, shade-tolerant species such as eastern hemlock and sugar maple. At a local scale within a forest, the effects of land use are dominant. For example, the variety and abundance of different trees vary substantially among areas that were permanent woodlots, pastured, or cropped (Foster 1992).

When species composition is examined, even patches of forest that seem mature and stable may be very unlike the forests that existed before the arrival of European settlers (Foster et al. 1992). A single woodland that remained forested throughout the settlement period has changed profoundly in tree species composition and structure during the past 250 years. The dominant species in the canopy have changed at least three times. Surprisingly, many of the trees that were common before European settlement are now rare within the woodland and uncommon in the landscape. Sugar maple and American beech have been almost completely eliminated locally because of land-use changes (Foster et al. 1992).

According to detailed vegetation and land-use analyses (White and Mladenoff 1994), similar transitions in forest composition have taken place in northern Wisconsin. Old-growth eastern hemlock and mature hardwood dominated a 9,600-hectare study landscape during the mid-1800's. By 1931, after large-scale logging and burning of the slash left behind, young forests covered more than 50% of the landscape. By 1989, the area was covered by a mixture of second-growth hardwood and conifer types. Regionally, the regrowing young forest closely resembles presettlement forest distribution, but the variety of trees has changed. A return to the formerly dominant hemlock forest in northern Wisconsin is not likely, based on current trends. Rather, there are two likely alternative directions leading toward either northern hardwoods or a boreal forest dominated by spruce, fir, and pines. Other midwestern oak forests are being converted to forests dominated by maples, black cherry, and yellow-poplar. This trend of reduced oak regeneration has also been documented in Pennsylvania (Abrams and Nowacki 1992) and Illinois (Iverson and Schwartz 1994). Thus, modern forests have not returned to their presettlement composition (Foster et al. 1992). Although the total area covered by forest has increased since 1900 across much of the eastern United States, today's forests are very different from those of the 1700's.

Forest Changes and Forest Animals

Animal communities have been profoundly affected by the removal and regrowth of forests—we know that animals inhabited places that would surprise us today (see MacLeish 1994). Bison used habitats ranging from the Great Plains all the way to Florida, grizzly bears ranged the Midwest, and elk roamed New England. Passenger pigeons, now extinct, flew in great flocks. Qualitative changes in the presence and abundance of animals during the past few centuries have been described. For example, predators such as wolves and furbearers such as beaver declined dramatically following settlement. French and Dutch fur traders in the Northeast took 30,000 beaver pelts in 1620 and almost 300,000 in 1690 (MacLeish 1994), but few such quantitative data exist. Although species have been lost and gained over past centuries, detailed studies have been conducted only in the past several decades.

Forest removal and regrowth create a series of young forest stages that change in space and time. Much of the young successional forest that dominated the landscape earlier during this century has declined markedly as these secondary forests approach maturity (Brooks and Birch 1988; Powell et al. 1993). Animals that thrive in early successional habitats also increased in abundance early in the century and are now declining. For example, as forest cover across the New England states increased to 75%–90% during the past century (Irland 1982), the New England cottontail declined substantially throughout its range (Chapman and Stauffer 1981); the pattern of decline correlated with losses of old fields and young forest habitats (Litvaitis 1993). Bobcats in New England experienced a simultaneous decline related to the decline of their early successional prey species (Litvaitis 1993).

Changes in bird abundances correlate with changes in early successional and forest cover. During the 1937–1989 period of reforestation in Massachusetts, 8 of 18 migratory bird species that declined are known to nest in early successional habitats (Hill and Hagan 1991). Since 1966 the eastern towhee—a species that prefers shrub cover, including abandoned agricultural fields—has declined 13% in the eastern United States (Hagan 1993). Between 1966 and 1988 in coastal New England, 9 of 18 species of nesting land birds associated with early successional habitats have declined (Witham and Hunter 1992). Agricultural land decreased by 9% and early successional habitats by 12% during the same period, while rural housing area increased 23% and urban–industrial land use increased 4%. Additionally, many New England breeding birds that winter in the Southeast have declined

significantly in recent years. It is possible that land-use change in the Southeast may be an important factor contributing to this decline as well (Hagan et al. 1991).

In contrast, forest birds may be rebounding as open habitats diminish. Nine of 15 species in coastal New England that have increased in numbers since 1966 were associated with closed canopy forests (Witham and Hunter 1992). From 1953 to 1976, changes in the bird community of a Connecticut forest preserve were correlated with changes in the abundance of forest in the surrounding landscape (Askins and Philbrick 1987). Forest birds in the preserve declined with forest removal in the surrounding landscape but began to increase again when forest cover increased. Bird species that thrive in residential areas also increased as the surrounding suburb expanded.

Although forested habitat has increased in some areas, today's forested habitats may not be as suitable for some native species when compared to the forested habitats of presettlement times. For example, the extensive deciduous forest that covered the southeastern Piedmont has been replaced by pine forests, which do not provide the conditions needed by various species—forest understory wildflowers and birds such as the red-eyed vireo—that thrived in the original deciduous forests. In the Midwest, old-growth forests and disturbed forests differ substantially in their spatial pattern across the landscape (Mladenoff et al. 1993). Compared with the large, continuous old-growth forests, the disturbed forests have numerous smaller patches of simple shape. Furthermore, certain habitat combinations—such as eastern hemlock forests aligned next to other conifer forests—occurred in the old-growth forest but are absent in the disturbed forests. Such habitat alignments are important for species that use edges or obtain resources from different habitat types (Dunning et al. 1992).

Aquatic and River Forest Losses Resulting From Land-Use Change

Wetlands, floodplains, and riparian vegetation zones have often been altered by agricultural and urban development (Fig. 9). Woody riparian vegetation once covered an estimated 30–40 million hectares in the contiguous United States (Swift 1974); at least two-thirds of that area has been converted to nonforest land uses, and only 10–14 million hectares remained in the early 1970's. Floodplain clearing for agriculture, urbanization, and water-resource development (especially channel modification and impoundment; see chapter on Water Use) is responsible for much of the loss of riparian forests. In many states of the arid West, the Midwest, and the Lower Mississippi River

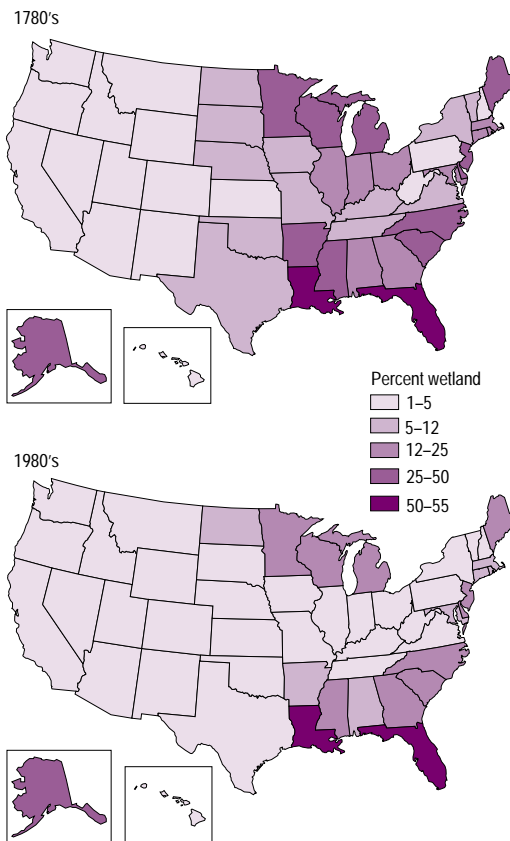


Fig. 9. Percentage of the areas of each state occupied by wetlands in the 1780's and the 1980's (adapted from Dahl 1990).

valley, riparian forests have been reduced by more than 80% (Swift 1974).

Sedell and Froggatt (1984) provide a classic example of the loss of riparian forest for the Willamette River, Oregon. Before 1850 the streamside forest extended up to 3 kilometers on either side of a river characterized by multiple channels, sloughs, and backwaters. By 1967 government-sponsored programs for forest clearing, snag removal, and channelization (channel deepening and straightening) reduced the Willamette River to a single uniform channel that had lost more than 80% of its forest and land-water edge habitats. Fresh waters are especially sensitive to changes in these adjacent lands (Osborne and Kovacic 1993). About 30% of the wetlands of the 50 states and 53% of the wetlands of the contiguous 48 states have been lost (Dahl 1990). The former wetlands slowed the flow of water, and their loss greatly increases the chances and severity of flooding. Wetland conversion also leads to loss of plant, wildlife, and fish species.

Fresh waters are degraded by increasing inputs of silt, nutrients, and pollutants from agriculture, forest harvest, and cities (Carpenter et al. 1996). Lakes and reservoirs fill more rapidly with mud from these sources. Moreover, the growth of nuisance plants, including toxic blue-green algae, is promoted by the increased silt and nutrients, a process called eutrophication. Within a lake or reservoir,

eutrophication is accompanied by a loss of desirable plants as the water becomes increasingly murky. Loss of native plants and chemical changes in the water lead to loss of animal species, including fishes and waterfowl. Regional changes in land use cause widespread eutrophication of many lakes on the landscape, thereby making the lakes more similar because they are all dominated by the same set of species that can tolerate eutrophic conditions. Thus, the diversity of lake types within a landscape is reduced as all lakes become eutrophic and harbor similar species (Carpenter et al. 1996).

Lake Mendota, Wisconsin, illustrates the losses of aquatic species that accompany land-use change in watersheds (Figs. 10–14). Before the advent of the plow in the 1830's, the watershed vegetation (Fig. 10) of this lake was prairie, oak savanna, and forest (Curtis 1959). Studies of dated layers of mud from sediment cores from the bottom of the lake show that the water quality of the lake was high before the rich prairie soils of the lake's drainage were plowed (Brock 1985; Hurley et al. 1992; Kitchell and Sanford 1992). By the 1870's the conversion of native vegetation to agriculture was essentially complete (Fig. 11), and towns were growing around the lake. Large blooms of annoying blue-green algae were common by the 1880's (Brock 1985), and dramatic changes in Lake Mendota's food web also occurred as the native plant communities were replaced by agriculture (Kitchell and Carpenter 1993). The most severe declines in water quality occurred after World War II (Lathrop 1992a) when the use of agricultural fertilizers increased substantially (Fig. 12). Cities also expanded to fill about 9% of the watershed (Fig. 13), and increasing amounts of sewage were added to the lake, intensifying eutrophication (Lathrop 1992a).

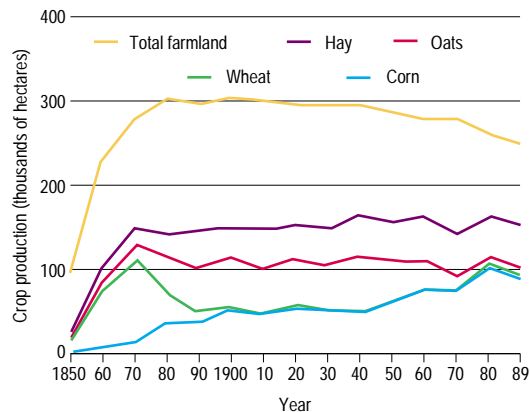


Fig. 11. Area of agricultural land use since 1850 in Dane County, Wisconsin, which includes the watershed of Lake Mendota (Lathrop 1992a).

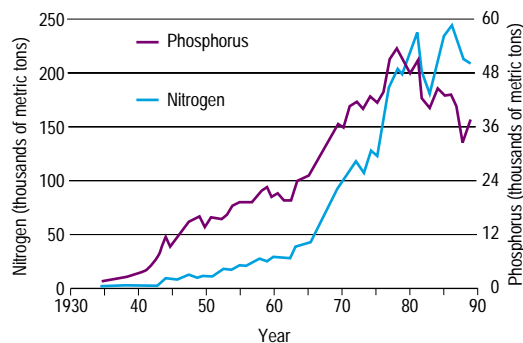


Fig. 12. Fertilizer use in Wisconsin from 1934 to 1989 (Lathrop 1992a).

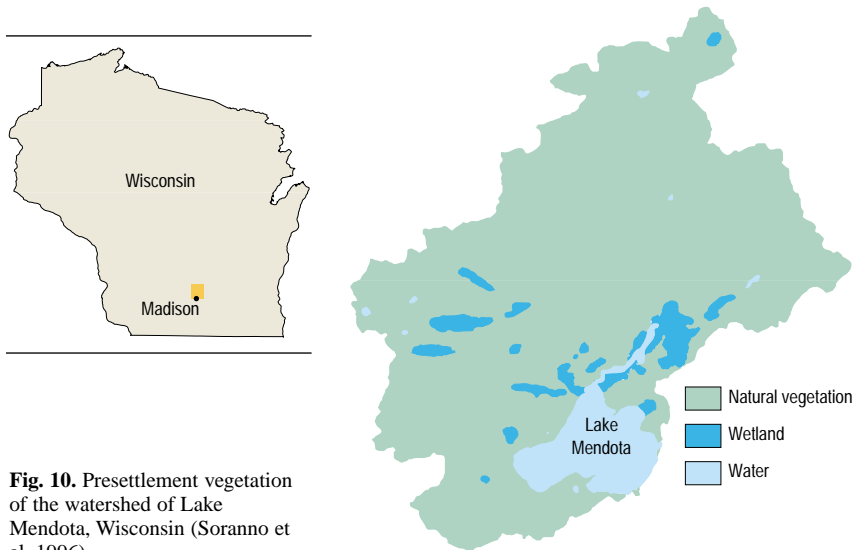


Fig. 10. Presettlement vegetation of the watershed of Lake Mendota, Wisconsin (Soranno et al. 1996).

Although losses of aquatic animals and plants have many interacting causes, most of the species losses from Lake Mendota occurred at the same time as did severe eutrophication, which was caused by increased cultivation, crop fertilization, and expansion of cities (Figs. 11–14). In 1946 the diversity of higher aquatic plants had probably changed little from presettlement times (Nichols et al. 1992), but by 1989, about half the species of aquatic plants were gone. The beds of wildcelery that once supported canvasbacks and other migratory waterfowl were lost, and the native pondweeds crucial for fish reproduction had also disappeared. These beneficial native plants were largely replaced by coontail and by Eurasian watermilfoil, a non-indigenous species, both of which have low food value for fishes and wildlife. Beginning around 1950, deepwater insect populations of Lake Mendota began a steep decline (Lathrop 1992b), and insect larvae—especially midges—that formerly supported fish production were almost absent from the deep waters of the lake by the mid-1960's. The long fingernailclam also disappeared. By the 1920's, six fish species had been eliminated because of intensive fishing and habitat loss. An additional five fish species

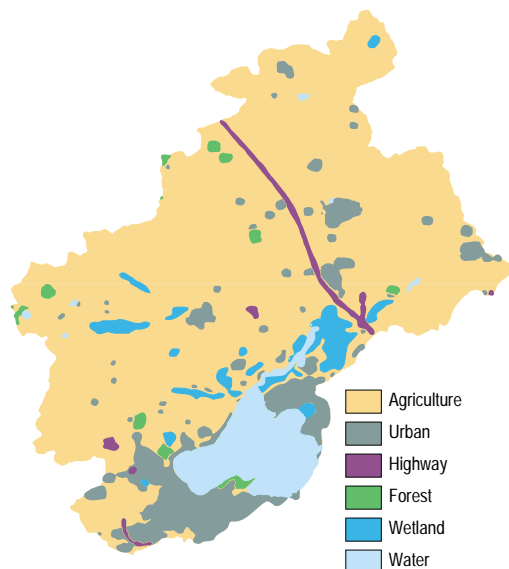


Fig. 13. Land-use patterns in the Lake Mendota, Wisconsin, watershed in 1990 (Soranno et al. 1996).

were lost by 1989 because of the disappearance of native aquatic plants and the stocking of predatory fish. Although 11 of the 37 fish species originally present in Lake Mendota have been extirpated, the lake now contains 37 fish species—the extirpated native species have been replaced by the introductions of fishes not native to the lake (Magnuson and Lathrop 1992).

Loss of native plants and animals is widespread in our nation's lakes, rivers, and other waters. The threat of a diminished variety of aquatic animals and plants is more serious than that for the variety of land animals and plants or even for the variety of organisms in tropical rain forests (Naiman et al. 1995). From 11% to 15% of the birds, mammals, and reptiles in the United States are classified as rare to extinct, but the proportion of aquatic animals and plants similarly classified is much higher—34% for fishes, 65% for crayfishes, and 75% for pearly-mussels (Master 1990). Of 214 stocks of Pacific salmon, 74% have a high or moderate risk of extinction (Nehlsen et al. 1991), primarily due to habitat loss from dams, logging, roads, and grazing (Forest Ecosystem Management Assessment Team 1993). Almost half (44%) of our nation's native clams and mussels are either extinct or endangered (Bogan 1993). Land-use-induced impoundment and inundation of riffle habitat in major river systems (such as the Ohio River, Tennessee River, Cumberland River, and Mobile Bay) and the disappearance of host fish species are responsible for the massive loss of native clams and mussels. About 82% of fishes in the United States are adversely affected by poor water quality, often resulting from habitat loss and fragmentation (Miller et al. 1989).

Secondary causes of fish decline are also important, including invasions of nonindigenous species, effects of pollutants, and overfishing. Of the 27 species and 13 subspecies of freshwater fishes that have become extinct in North America during the last century, habitat degradation contributed to at least 73% of these extinctions. The losses of aquatic plants and animals may not be apparent to the casual observer (Noss et al. 1995), but present-day lakes, rivers, and streams are substantially different from those encountered by the early settlers.

Implications of Present Land-Use Patterns for Biological Diversity

Past, present, and future land-use patterns will continue as a dominant influence on biological diversity in the United States. What general themes emerge from our understanding of past land-use changes, their effects on plants and animals, and their importance for understanding the effects of current land-use patterns? We highlight four related issues regarding land use and biological diversity that will continue to be important in coming decades: pervasive effects of habitat fragmentation, indirect effects of land-use change, the importance of landscape context, and land-use practices.

Pervasive Effects of Habitat Fragmentation

Continued habitat fragmentation is one of the most important results of recent land-use changes. Agricultural land conversion has indeed slowed during recent decades, although suburban development, which accelerated nationwide after World War II, still continues unabated. Urban and suburban developments have resulted in loss and fragmentation of natural habitats in many regions of the United States. Resource extractions such as logging, mining, and oil drilling have also resulted in habitat fragmentation.

Adverse effects of fragmentation on biological diversity have been documented by many studies (see Saunders et al. 1991; Noss and Csuti 1994). Of course, species may be directly eliminated from portions of the landscape where habitat has been converted to other uses, but the size of remaining fragments of habitat influences the number of species that can live within each fragment. Small forest patches in Maryland had fewer nesting bird species than larger patches (Whitcomb et al. 1981; Lynch and Whigham 1984); furthermore, species that nested in interior regions of a forest (that is,

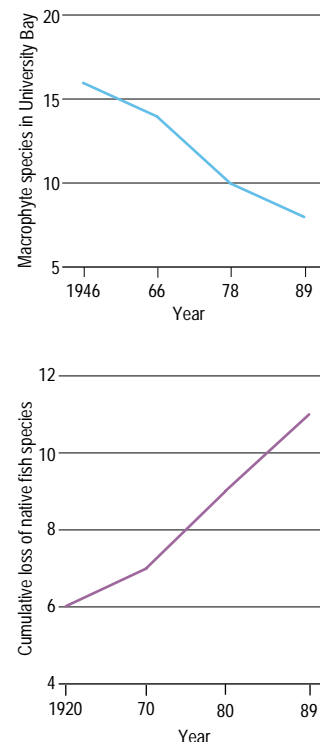


Fig. 14. Change in species richness of aquatic plants and cumulative loss of fishes from Lake Mendota, Wisconsin, during the 1900's (Magnuson and Lathrop 1992; Nichols et al. 1992).

away from the forest edge) were unlikely to inhabit forest patches smaller than a certain size (Whitcomb et al. 1981). Most species lost from small patches were insect-eating birds that migrate to tropical regions of North and Central America. Individual birds that inhabit small forest patches also may have difficulty finding mates (Villard et al. 1993) because fewer birds are present.

The size and arrangement of habitat fragments also affect how animals use the space around them. For example, red squirrels in forest fragments had reduced home ranges in small forest patches (Wauters et al. 1994); the squirrels' use of forest resources was influenced by the size and shape of patches and the presence of connecting corridors among patches. Negative effects of fragmentation have been recorded in midwestern forests (Gottfried 1979) and grasslands (Glenn and Collins 1992; Herkert 1994), the Rocky Mountains (Keller and Anderson 1992), and western forests (Harris 1984).

Loss of old-growth forest is another noteworthy case of habitat fragmentation. Little old-growth forest remains in the lower United States, and species that require the remaining rare old-growth forests will continue to be at risk as land use continues to change. There appear to be no species dependent on old-growth forests in the East today, but old-growth obligates probably disappeared long ago and may have included the ivory-billed woodpecker and Bachman's warbler. The apparent dependency of the northern spotted owl and marbled murrelet on the old-growth forests of the West Coast has ignited an intense controversy over timber harvesting in western forests (Simberloff 1987). The concern centers on both the absolute loss of old-growth habitat and how disconnected the remaining habitat patches have become. Because fragmentation of habitat makes dispersal more difficult and reduces population stability (Lande 1988; Doak 1989), the pattern of timber harvest activity has important consequences (Franklin and Forman 1987). A common practice on national forests in the Pacific Northwest had been to maximize spacing of clear-cuts, leading to a highly fragmented forest condition that persists for many years (Wallin et al. 1994). Consequently, species that require large areas of old-growth or interior forest are thought to be at risk because of these logging practices, particularly the widespread spacing of clear-cuts throughout the forest.

Land-use activities also introduce new human-dominated habitat types such as roads, which may disconnect natural habitats. Road length and area increase with land development,

and roads can be effective barriers to the movements of animals, especially invertebrates and smaller vertebrates. Mader (1984) demonstrated the almost complete division of populations of a forest-dwelling ground beetle by a road and parking loops. Of 387 small rodents that were tagged and recaptured during an extensive study on the effects of a highway in the Mojave Desert, only one was found on the opposite side of the road (Garland and Bradley 1984). Large animals are also susceptible to road effects. Grizzly bears in the northern Rocky Mountains used areas within 100 meters of roads less frequently than areas away from roads; this resulted in a nearly 9% loss of prime bear habitat (McLellan and Shackleton 1988). Roads also increased the bears' vulnerability to poachers and legal hunters. In northern Wisconsin, wolves were much more likely to use portions of the landscape where road density was lowest (Mladenoff et al. 1995). In Florida, the highway system presents both a significant barrier to movement and a cause of death for the endangered Florida panther. Even when behavioral responses (such as avoidance) to roads have been observed, the long-term effects of roads on population size and population growth rates are not known and require further study.

Many questions remain about the effects of habitat fragmentation, especially because habitat fragmentation affects different species in different ways (Robinson et al. 1992). In a study of an arthropod (joint-legged animals such as crabs, spiders, and insects) community, an amphipod population declined severely in small habitat patches, but habitat size had no effect on a scorpion (Margules et al. 1994). Some authors (for example, Haila et al. 1993) have argued that the lower numbers of species observed in small habitat patches are simply due to chance. For example, McCoy and Mushinsky (1994) found more vertebrate species in large patches of Florida scrub habitat, but when the effect of patch area was removed from the data, the small patches did not have significantly fewer species.

The fragmentation—or connectivity—of a habitat depends on both its abundance and spatial arrangement. Land-use changes generally alter both the area and configuration of habitats. If habitats decrease in area, effects on plants and animals are aggravated if the habitat also becomes fragmented. Fragmentation can result in the loss of species in single habitat patches as well as loss from the regional landscape. Land-use planning can minimize the effects of habitat loss by maintaining large blocks of native habitat and protecting natural corridors—such as river forest corridors and ridgetops—that connect the remaining large habitat blocks.

Indirect Effects of Land-Use Change

Land-use patterns and habitat fragmentation can initiate a chain of events that leads to unexpected effects. In some instances, the relative abundances of different species change in response to land use, and this in turn causes other organisms to respond. These occurrences can be considered as indirect effects because the land-use activity starts a series of events in which the final result may be unexpected. For example, elevated densities of organisms that thrive in fragmented landscapes have triggered chain reactions that affect many other species. The large numbers of many herbivores (animals that eat plants) that presently occupy our landscapes are a consequence of past land use as well as the government-sponsored predator removals of the early 1900's. Declines of species that play important roles in the ecosystem can also start a chain reaction that affects other species. For example, land-use changes on the Coastal Plain have resulted in loss of habitat for gopher tortoises. Decline of this species may cause reductions or losses of many other species because nearly 400 species of invertebrates and vertebrates have been found in gopher tortoise burrows (Noss et al. 1995).

Densities of white-tailed deer have reached unprecedented levels in many parts of the Northeast (McCabe and McCabe 1984; Witmer and deCalesta 1992; Parker and Van Kley 1993; Correll 1994). These high levels are largely due to the widespread increases in early successional habitats, the added edge habitat between forested and nonforested lands, and the reduced predation and hunting since the 1930's. Land-use changes in the past century provided bonus habitat for deer, but their overabundance has led to deleterious consequences for many other species. The high numbers of deer first influence vegetation structure and composition because the larger deer population consumes more food. Browsing damage by deer can result in significant loss of species and abundance of woody and herbaceous plants (Kroll et al. 1986; Alverson et al. 1988; Tilghman 1989; Miller et al. 1992). Deer damage can become so severe in preserves where hunting is prohibited (for example, state parks and research forests) that seedlings of trees, shrubs, and woody vines are almost completely eliminated. In preserves with dense deer populations, wildflower and grassy cover may be less than 65% of that outside the preserves (Parker and Van Kley 1993; Correll 1994). Because the number of species and abundance of forest songbirds depend on woody vegetation (MacArthur and MacArthur 1961; Karr and Roth 1971), songbird populations are depressed by high deer numbers (Casey and Hein 1983; McShea and Rappole 1992;

deCalesta 1994). Clearly, land-use patterns play an important role in this story. Reduction of forest edge to reduce deer densities has been proposed (Alverson et al. 1988), but any successful solution must likely include reduction of deer numbers by hunting (Alverson et al. 1988; deCalesta 1994).

When forests are fragmented, forest birds experience higher rates of parasitism by brown-headed cowbirds—another species that thrives and increases with forest clearing. Cowbirds lay their eggs in the nests of other bird species, and the young cowbirds effectively commandeer the food and attention of the host parents, usually at the expense of the host's own offspring. Cowbirds feed almost exclusively in open short-grass habitats, so the frequency of parasitism is primarily influenced by the amount and type of open land near the nest site (Brittingham and Temple 1983; Robinson 1992). Cowbird nest parasitism is generally limited to areas within 7 kilometers of feeding sites (Rothstein et al. 1984), although average commuting distances are usually much less (Robinson et al. 1993; Thompson 1994). Parasitism rates are generally higher near forest edges (Brittingham and Temple 1983; Yahner and Scott 1988). Nationwide, cowbirds became rarer away from the center of their range in the Great Plains and also declined as the proportion of a landscape in forest increased (Thompson et al. 1996). In the Midwest, cowbird abundance and parasitism were lower in areas with more total forest, more forest interior, and larger forest patches (Thompson et al. 1996).

Almost by definition, indirect effects of land-use change can be difficult to anticipate. These effects are passed along through the intricate web of interactions among species and may take many years to appear. It is important to recognize, though, that there may be significant and surprising long-term consequences from inducing large changes in the abundance of species.

Importance of Landscape Context

The animals and plants contained within habitat patches are affected by what is around them—that is, the context of the surrounding landscape (Askins and Philbrick 1987; Pearson 1993). Better understanding of this broad-scale influence is sorely needed, and it must be considered in land-use decisions. Landscape context is important because the biological diversity of parks, preserves, and wildlife corridors may be affected by changes in the regional landscape (Franklin 1993). For example, the ability of a species to disperse to a particular habitat patch will depend on whether the surrounding landscape makes movement easier or more

difficult (Taylor et al. 1993). Harsh and unsuitable habitats in the landscape may present barriers to species movements. River forests are often protected to maintain water quality and to provide wildlife habitat, but the effectiveness of river forest corridors is influenced by the surrounding upland landscape. For example, the species of birds found in river forest corridors are different depending on whether the surrounding landscape is forested or agricultural (Croonquist and Brooks 1993) or whether it is in the country or the city (Smith and Schaefer 1992). Urbanization of the surrounding landscape also affects other natural habitats, such as woodlots (Whitcomb et al. 1981; Tilghman 1987). The effect of cowbirds in forests, for example, depends on the presence of open feeding habitats in the broader landscape (for example, Gustafson and Crow 1994). Thus, interpretation or projection of trends in terrestrial species must consider the broader landscape.

The importance of the landscape for aquatic systems is paramount. Freshwater quality and biological diversity depend on riverine forests and floodplains that slow the transport of water, retain silt and nutrients, and provide spawning sites, food, and shelter for fishes and wildlife. Diverse, self-sustaining river and lake-edge vegetation is crucial to the quality of lakes and streams. Logging, cultivation, or residential development of river- or lake-edge forests accelerate water flow, increase soil erosion, and eliminate habitat. Such changes in these forests thereby result in significant costs in wildlife, fishes, and downstream water quality. Once the forests at the edges of rivers or lakes are significantly changed, restoration may be very difficult and extremely expensive. Thus, decisions about river- and lake-edge land use should consider costs to wildlife, fishes, water quality, and the potential permanent problems caused by development. Wetland, floodplain, and riparian restorations, which are sorely needed in many areas of the United States (National Research Council 1992), should be ranked by comparing the costs and benefits of each project. Benefits need to accumulate at the level of watersheds or even larger spatial units, and this scale must be considered in the accounting process.

Land-Use Practices

Actual land-use practices, of course, affect biological diversity. Forest-cutting methods and fire reduction serve here as examples that illustrate this occurrence. However, the ways developments are sited and built, how lands are used for grazing, and the ways in which agriculture is practiced are other ways in which land-use practices are important.

Several different logging methods are widely used in North America; these have fairly predictable consequences on the structure and pattern of habitats. Even-age methods result in stands composed of trees of a single age class, while uneven-age systems periodically remove trees to maintain a variety of different ages of trees within the stand (Thompson et al. 1993). The effects of these logging methods on forest birds have been studied in ecosystems throughout the country (Conner and Adkisson 1975; Crawford et al. 1981; Steffen 1985; Thompson and Fritzell 1990; Dickson et al. 1993; Hutto et al. 1993; Thompson 1993). The common finding of all these studies is that, in the short term, logging enhances habitat for some species and degrades habitat for others. Openings produced by even-age logging upset the continuity of closed canopy forest and may have negative effects on birds of the forest interior (Perneluzi et al. 1993). Some logging methods produce so many small, dispersed openings that interior forest conditions are very difficult to maintain (Gustafson and Crow 1994). The edges produced by even-age harvests and group selection may increase predation and brood parasitism rates so much that bird reproduction is seriously reduced (Paton 1994). Uneven-age methods do allow retention of mature forest bird communities, though at lower densities than in unmanaged forests. Nevertheless, uneven-age harvest methods do not produce the same level of landscape diversity of old and young forest patches that characterizes natural forests (Dickson et al. 1993; Thompson et al. 1993).

The short-term effects of logging on bird populations have been the subject of many studies, but long-term consequences are not as well known. For example, clear-cutting may cause profound short-term changes in forests, but these changes may be critical to a long-term approach for maintaining the kind of historical ecological conditions dependent on widespread, frequent disturbances such as fire (Hunter 1992; Hutto et al. 1993; Reice 1994). The long-term effects of excluding large-scale natural disturbances from ecosystems are not well known because such protection has been relatively recent.

Concern has recently been raised about the effects of logging on land-dwelling salamanders (Petranka et al. 1993) and nonwoody plants of the forest understory (Duffy and Meier 1992). There is no general agreement on the effects of land-use practices on plants and animals that have not been well studied; these species deserve continued investigation (Elliott and Loftis 1993; Johnson et al. 1993).

Sometimes land-use practices alter the natural disturbance regimes that generate the

complex patterns of habitats required by native plants and animals. If land-use practices change the frequency, size, and intensity of natural disturbances, then altered sequences of vegetation development may lead to completely different plant communities (see chapter on Natural Processes for a complete discussion of disturbance regimes). For example, although eastern oak–hickory forests were traditionally thought of as a stable climax forest community (Weaver and Clements 1938; Braun 1950), they are now being succeeded by moist forests dominated by hard maples (Schmelz et al. 1975; Lorimer 1985; Schlesinger 1989). This trend has been attributed to the reduction in natural fire caused by fire control during the twentieth century (Curtis 1959; Lorimer 1985; Van Lear and Waldrop 1989). Periodic fires enable oaks to become dominant among competing species (Rouse 1986), and the oaks cannot replace themselves without disturbance (Kessler 1992).

Forest composition in the Southeast is also dominated by disturbance-initiated species and has been attributed to human activity over the last one or two thousand years (Buckner 1989). The exclusion of fire and major disturbance in many eastern forest systems is relatively recent and may now be producing completely new combinations of plant communities in certain regions. The abilities of animal species to adapt to these new plant communities are unknown. Clearly, the ways in which land is managed for particular uses will continue to influence the plants and animals that are present.

Land Use and Biological Diversity: Important Next Steps

Serious environmental problems often come as surprises. Some of the more obvious symptoms of environmental degradation in the United States are now being addressed through public or private management actions. But what is the likely origin of the next environmental surprise? When examined in retrospect, some surprises have come from incremental shifts that crossed a threshold to catastrophic change. Such big effects from small causes (Ricker 1963) are known from many natural and social systems (Holling 1978). We suggest that it is the accumulation of small local changes that poses the greatest long-term challenge to encouraging sustainable land-use patterns in the United States.

Individual changes in land use may appear to have only local significance. In total, however, the large number of local changes is transforming the landscape of the United States. Gradual but widespread change leads to significant

effects on vegetative cover, wildlife habitat, soils, and water quality. If the current path of land use in the United States continues, we can expect continued loss of wildlife and vegetation, erosion of soils, and nonpoint pollution of groundwater and surface water. If we are willing to manage landscapes for the larger good, these losses can be prevented, and the resources can be restored. Progress will require adaptive change and planning, monitoring, and research. Most importantly, it requires the political will to maintain a landscape that supports the natural resources we expect and need.

Present trends in land use suggest that collisions between the desires of the human population and natural ecological processes will continue. Ongoing urban development in our landscapes—including suburban sprawl and development of vacation homes—locks a pattern onto the landscape that is hard to reverse. Many farms of the previous century have been returning to more natural vegetation, but urban and suburban areas are more permanent. The larger lot sizes and the more sprawling nature of subdivisions that extend well into the countryside are an increasingly important cause of habitat loss and fragmentation. Housing located near natural areas may be quite desirable for the views and the privacy afforded; however, as a result of this practice, encounters between humans and wild animals or conflicts over the management of natural fires intensify. Developments are often designed to transport water off the land as quickly as possible, so developed watersheds become more prone to flooding. The fragmentation of large blocks of habitat can be minimized by the clustering of similar land uses, which has important implications for cities and suburbs. In general, it is more beneficial for habitat connectivity if human activities are concentrated than if they are dispersed widely throughout the landscape.

Land managers must enlarge their perspective to encompass the landscape. Clearly, plants and animals respond to regional patterns and to changes in habitat availability and connectivity. Natural disturbances, which create patchiness and structure biotic communities, must also be considered. Managers of natural areas that do not consider the surrounding seminatural environments lose crucial opportunities for maintaining more extensive habitats that harbor richer arrays of native plants and animals (Franklin 1993). When land managers focus too closely and don't "see the forest for the trees," the benefits of biological diversity may be lost. Management of freshwater habitat, for example, is likely to fail if the important riparian animals and plants are neglected or if land use in the floodplains is ignored. Land management should become a more cooperative venture that

works within ecologically meaningful boundaries rather than political or jurisdictional boundaries.

Effective conservation of aquatic ecosystems and their biological diversity also requires a landscape perspective (National Research Council 1992). Unfortunately, most attempts to manage or restore aquatic systems address isolated components—for example, individual lakes, rivers, or wetlands. Agency responsibilities are oriented toward components rather than whole ecosystems (Leopold 1990), and the expertise needed for restoration is divided among various disciplines (National Research Council 1992). In practice, this division creates problems because uplands, wetlands, groundwater, rivers, lakes, and estuaries are interconnected by flows of water and nutrients and by migrations of organisms. These connections, though, must be considered. For example, wetlands are often essential to restoring lakes, but well-intentioned lake management (such as water level stabilization) could harm the wetlands. Pragmatic approaches to managing aquatic ecosystems require coordination at the watershed or landscape scale. At present, no organization or institution in the United States is responsible for the integrated view that makes watershed restoration practical (Cairns 1994). Addressing this challenge would benefit us all.

Species do not recognize political boundaries, suggesting the potential for considering some degree of integrated management of the natural and seminatural landscape. Of course, land-use regulation is a potentially explosive issue. A solution to balancing human needs and maintenance of biological diversity is not ecologically sustainable unless it is also politically sustainable. Forcing landowners to enhance biological diversity by regulation will probably produce a backlash that could lead to long-term loss of species. Research should proceed on the development of market-based incentives that encourage maintenance of species and habitats. Perhaps the greatest challenge for biological diversity protection is to preserve the structure and function of native ecosystems while protecting the rights and privileges of private property owners.

Many questions remain about the past and future effects of land use on animals and plants, and a few research needs stand out. Because the pattern of habitats across the landscape has such a strong influence on native animal and plant communities, improvements in methods for predicting future land-use patterns are sorely needed. Predicting land-use change requires linking knowledge and techniques from numerous disciplines, including economics, sociology, and ecology (Lee et al. 1992; Turner et al. 1996; Wear et al. 1996). Such interdisciplinary study is

naturally complex, but there should be strong encouragement to develop the required integration. Better understanding is needed of what drives land-use change and how land-use patterns will respond to changing human population growth. Predictions of land-use change also should include not only the amount of change but also how the changes are arranged across the landscape. The effects of patch size and habitat fragmentation are sufficiently important that models should incorporate these factors (Turner et al. 1995). Models are a crucial component of research geared toward land use and biological diversity. Models permit us to project effects on plants and animals of the land-use experiments that society is presently conducting and to explore alternative future scenarios.

Greater explanation of what caused the pattern of plants and animals across today's landscapes is needed. The extent to which observed changes in present-day plant and animal communities are due to effects caused by changes in land-use practices decades ago or are directly related to recent practices is unclear. Some effects of past land use may persist for many decades, especially if long-lived organisms like trees are considered. In addition, the degree to which natural successional trajectories have been permanently altered by land use is not known. For example, the endpoints of the changing forest composition observed in the East and upper Midwest are not known. Many more empirical studies relating land-use change to biological diversity would be valuable, and more case studies would improve general understanding, as well as better explain local biotic patterns. These are important needs for relating land-use changes in the future to expected species' responses.

The most remarkable aspect of the landscape of the United States since European settlement is its continually changing face. Effects of these vast changes are long-lasting and crucial to our understanding of the present-day plants and animals that inhabit our landscapes (Foster 1992). In turn, conservation remains challenging in part because we seek to preserve areas that are changing (White and Bratton 1980). Ecological systems do not exhibit an undisturbed state that can be maintained indefinitely, but land use can alter both the rate and direction of natural trajectories. Because land-use patterns create the environment in which plants and animals must live, reproduce, and disperse, our understanding of the influence of land use on biological diversity is critical to the future of land management. The question is not whether we should or should not use land, but rather how we can best use the land. Open lands in the United States still abound in many areas. We are not predestined to continue past trends in land use. Rather,

Authors

Monica G. Turner
Department of Zoology
University of Wisconsin
Madison, Wisconsin 53706

Stephen R. Carpenter
Center for Limnology and
Department of Zoology
University of Wisconsin
Madison, Wisconsin 53706

Eric J. Gustafson
U.S. Forest Service
Forestry Sciences Laboratory
5985 Highway K
Rhinelander, Wisconsin 54501

Robert J. Naiman
Center for Streamside Studies
University of Washington
Seattle, Washington 98195

Scott M. Pearson
Department of Biology
Mars Hill College
Mars Hill, North Carolina 28754

we have the opportunity to choose our destiny and plan for quality growth, balancing human needs while maintaining the integrity of our nation's primary resource—the land.

Acknowledgments

We especially thank J. Fraterrigo for her timely assistance with the library research required for this chapter. Comments from

L. Iverson, J. Magnuson, and an anonymous reviewer improved the manuscript. This research was funded by the National Biological Service. The National Science Foundation also contributed to the ideas developed here through funding to the Coweeta and North Temperate Lakes Long-term Ecological Research Sites.

Cited References

- Abrams, M. D., and G. J. Nowacki. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bulletin of the Torrey Botanical Club* 119:19–28.
- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests to deer: edge effects in northern Wisconsin. *Conservation Biology* 2:348–358.
- Anderson, R. C. 1970. Prairies in the Prairie State. *Transactions of the Illinois State Academy of Science* 63:214–221.
- Anderson, R. C., and J. E. Schwegman. 1991. Twenty years of vegetational change on a southern Illinois barren. *Natural Areas Journal* 11:100–107.
- Askins, R. A., and M. J. Philbrick. 1987. Effect of changes in regional forest abundance on the decline and recovery of a forest bird community. *Wilson Bulletin* 99:7–21.
- Barrows, H. 1910. Geography of the middle Illinois valley. State Geological Survey, Bulletin 15. 127 pp.
- Bogan, A. E. 1993. Freshwater bivalve extinctions. *American Zoologist* 33:599–600.
- Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Press, New York. 596 pp.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35.
- Brock, T. D. 1985. A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York. 308 pp.
- Brooks, R. T., and T. W. Birch. 1988. Changes in New England forests and forest owners: implications for wildlife habitat resources and management. *Transactions of the North American Wildlife and Natural Resources Conference* 53:78–87.
- Buckner, E. R. 1989. Evolution of forest types in the Southeast. Pages 27–33 in T. A. Waldrop, editor. *Proceedings of pine-hardwood mixtures: a symposium on management and ecology of the type*. U.S. Forest Service, Southeastern Forest Experiment Station, Asheville, N.C.
- Bureau of the Census. 1990. Statistical abstract of the United States, 1990: the national data book. U.S. Department of Commerce, Washington, D.C. 991 pp.
- Burgess, R. L., and D. M. Sharpe, editors. 1981. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York. 310 pp.
- Cairns, J. 1994. Eco-societal restoration: re-examining human society's relationship with natural systems. Abel Wolman Distinguished Lecture, Water Sciences and Technology Board, U.S. National Academy of Sciences, Washington, D.C.
- Carpenter, S., T. Frost, L. Persson, M. Power, and D. Soto. 1996. Freshwater ecosystems: linkages of complexity and processes. Chapter 12 in H. A. Mooney, editor. *Functional roles of biodiversity: a global perspective*. John Wiley & Sons, New York.
- Casey, D., and D. Hein. 1983. Effects of heavy browsing on a bird community in a deciduous forest. *Journal of Wildlife Management* 47:829–836.
- Chapman, J. A., and J. R. Stauffer. 1981. The status and distribution of the New England cottontail. Pages 973–983 in K. Myers and C. D. MacInnes, editors. *Proceedings of the world lagomorph conference*. University of Guelph, Ontario, Canada.
- Charbonneau, R., and G. M. Kondolf. 1993. Land use change in California, U.S.A.: nonpoint source water quality impacts. *Environmental Management* 17:453–460.
- Conner, R. N., and C. S. Adkisson. 1975. Effects of clear-cutting on the diversity of breeding birds. *Journal of Forestry* 73:781–785.
- Cooper, C. F. 1960. Changes in vegetation, structure and growth of southwestern pine forests since white settlement. *Ecological Monographs* 30:129–164.
- Correll, D. L. 1994. Draft environmental assessment: public deer hunting on lands of the Smithsonian Environmental Research Center. Proposal, Smithsonian Environmental Research Center, Edgewater, Md.
- Crawford, H. S., R. G. Hooper, and R. W. Titterton. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. *Journal of Wildlife Management* 45:680–692.
- Croonquist, M. J., and R. P. Brooks. 1993. Effects of habitat disturbance on bird communities in riparian corridors. *Journal of Soil and Water Conservation* 48:65–70.
- Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, Wis. 657 pp.
- Dahl, T. E. 1990. Wetlands losses in the United States, 1780's to 1980's. U.S. Fish and Wildlife Service, Washington, D.C. 13 pp.
- deCalesta, D. S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58:711–718.
- Denevan, W. M. 1992. The pristine myth: the landscape of the Americas in 1492. *Association of American Geographers* 82:369–385.
- DeVivo, M. S. 1990. Indian use of fire and land clearance in the southern Appalachians. Pages 306–310 in S. C. Nodvin and T. A. Waldrop, editors. *Fire and the environment: ecological and cultural perspectives*. U.S. Forest Service General Technical Report SE-69.
- Dickson, J. G., F. R. Thompson III, R. N. Conner, and K. E. Franzreb. 1993. Effects of silviculture on Neotropical migratory birds in central and southeastern oak pine forests. Pages 374–385 in D. M. Finch and P. W. Stangel, editors. *Status and management of Neotropical migratory birds*. U.S. Forest Service General Technical Report RM-229.
- Doak, D. 1989. Spotted owls and old growth logging in the Pacific Northwest. *Conservation Biology* 3:389–396.
- Duffy, D. C., and A. J. Meier. 1992. Do Appalachian understories ever recover from clearcutting? *Conservation Biology* 6:196–201.
- Dunn, C. P., D. M. Sharpe, G. R. Guntenspergen, F. Stearns, and Z. Yang. 1991. Methods for analyzing temporal changes in landscape pattern. Pages 173–198 in M. G. Turner and R. H. Gardner, editors. *Quantitative methods in landscape ecology*. Springer-Verlag, New York.
- Dunning, J. B., J. B. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175.
- Elliott, K. J., and D. L. Loftis. 1993. Vegetation diversity after logging in the southern Appalachians. *Conservation Biology* 7:220–221.

- Fedkiw, J. 1989. The evolving use and management of the nation's forests, grasslands, croplands and related resources. U.S. Forest Service General Technical Report RM-175.
- Forbes, S. A. 1913. The midsummer bird life of Illinois: a statistical study. Illinois Laboratory of Natural History Bulletin 9:266–270.
- Forbes, S. A., and A. O. Gross. 1922. The numbers and local distribution in summer of Illinois land birds of the open country. Illinois Laboratory of Natural History Bulletin 14:187–218.
- Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: an ecological, economic and social assessment. Report of the Forest Ecosystem Management Assessment Team. U.S. Forest Service, Washington, D.C. 1100 pp.
- Foster, D. R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, U.S.A. *Journal of Ecology* 80:753–772.
- Foster, D. R., T. Zebryk, P. Schoonmaker, and A. Lezberg. 1992. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. *Journal of Ecology* 80:773–786.
- 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.
- Garland, T., and W. G. Bradley. 1984. Effects of a highway on Mojave Desert rodent populations. *American Midland Naturalist* 111:47–56.
- Glenn, S. M., and S. L. Collins. 1992. Effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos* 63:273–280.
- Glitzenstein, J. S., C. D. Canham, M. J. McDonnell, and D. R. Streng. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. *Bulletin of the Torrey Botanical Club* 117:106–122.
- Gottfried, B. M. 1979. Small mammal populations in woodlot islands. *American Midland Naturalist* 102:105–112.
- Graber, R. R., and J. W. Graber. 1963. A comparative study of bird populations in Illinois, 1906–1909 and 1956–1958. *Illinois Natural History Survey Bulletin* 28:383–528.
- Gustafson, E. J., and T. R. Crow. 1994. Modeling the effects of forest harvesting on landscape structure and the spatial distribution of cowbird brood parasitism. *Landscape Ecology* 9:237–248.
- Hagan, J. M. 1993. Decline of the rufous-sided towhee in the eastern United States. *Auk* 110:863–874.
- Hagan, J. M., III, T. L. Lloyd-Evans, J. L. Atwood, and D. S. Wood. 1991. Long-term changes in migratory landbirds in the northeastern United States: evidence from migration capture data. Pages 115–130 in J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of Neotropical migratory landbirds*. Smithsonian Institution Press, Washington, D.C.
- Haila, Y., I. K. Hanski, and S. Raivio. 1993. Turnover of breeding birds in small forest fragments: the sampling colonization hypothesis corroborated. *Ecology* 74:714–725.
- Harris, L. D. 1984. *The fragmented forest*. University of Chicago Press, Ill. 211 pp.
- Herkert, J. R. 1991. Prairie birds of Illinois: population response to two centuries of habitat change. *Illinois Natural History Survey Bulletin* 34:393–399.
- Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* 4:461–471.
- Hill, D. B. 1985. Forest fragmentation and its implications in central New York. *Forest Ecology and Management* 12:113–128.
- Hill, N. P., and J. M. Hagan III. 1991. Population trends of some northeastern North American landbirds: a half-century of data. *Wilson Bulletin* 103:165–182.
- Holling, C. S. 1978. Myths of ecological stability: resilience and the problem of failure. *Journal of Business Administration* 4:97–109.
- Hunter, M. L., Jr. 1992. Paleocology, landscape ecology, and conservation of Neotropical migrant passerines in boreal forests. Pages 511–523 in J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of Neotropical migratory landbirds*. Smithsonian Institution Press, Washington, D.C.
- Hurley, J. P., D. E. Armstrong, and A. L. DuVall. 1992. Historical interpretation of pigment stratigraphy in Lake Mendota sediments. Pages 49–68 in J. F. Kitchell, editor. *Food web management: a case study of Lake Mendota*, Wisconsin. Springer-Verlag, New York.
- Hutto, R. J., S. J. Hejl, C. R. Preston, and D. M. Finch. 1993. Effects of silvicultural treatments on forest birds in the Rocky Mountains: implications and recommendations. Pages 386–391 in D. M. Finch and P. W. Stangel, editors. *Status and management of Neotropical migratory birds*. U.S. Forest Service General Technical Report RM-229.
- Irland, L. C. 1982. *Wildlands and woodlots—a story of New England forests*. University Press of New England, Hanover, N.H. 217 pp.
- Iverson, L. R. 1988. Land-use changes in Illinois, U.S.A.: the influence of landscape attributes on current and historic land use. *Landscape Ecology* 2:45–61.
- 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., and M. Schwartz. 1994. *Forests*. Pages 33–66 in Illinois Department of Energy and Natural Resources, the changing Illinois environment: critical resources. Volume 3. Technical Report ILENR-EA-94/05. Illinois Department of Energy and Natural Resources, Springfield.
- Johnson, A. S., W. M. Ford, and P. E. Hale. 1993. The effects of clear-cutting on herbaceous understories are still not fully known. *Conservation Biology* 7:433–435.
- Johnson, W. C., and D. M. Sharpe. 1976. An analysis of forest dynamics in the northern Georgia Piedmont. *Forest Science* 22:307–322.
- Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. *American Naturalist* 105:423–435.
- Keller, M. E., and S. H. Anderson. 1992. Avian use of habitat configurations created by forest cutting in southeastern Wyoming. *Condor* 94:55–65.
- Kessler, K. J., Jr. 1992. Oak decline on public lands in the central forest region. U.S. Forest Service Research Note NC-362. 4 pp.
- Kitchell, J. F., and S. R. Carpenter. 1993. Variability in lake ecosystems: complex responses by the apical predator. Pages 111–124 in M. J. McDonnell and S. T. A. Pickett, editors. *Humans as components of ecosystems*. Springer-Verlag, New York.
- Kitchell, J. F., and P. R. Sanford. 1992. Paleolimnological evidence of food web dynamics in Lake Mendota. Pages 31–48 in J. F. Kitchell, editor. *Food web management: a case study of Lake Mendota*, Wisconsin. Springer-Verlag, New York.
- Kroll, J. C., W. D. Goodrum, and P. J. Behrman. 1986. Twenty-seven years of over-browsing: implications to white-tailed deer management on wilderness areas. Pages 294–303 in D. K. Kulhavy and R. N. Conner, editors. *Wilderness and natural areas in the eastern United States: a management challenge*. Center for Applied Sciences, School of Forestry, Stephen F. Austin University, Nacogdoches, Tex.
- Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75:601–607.
- Lathrop, R. C. 1992a. Nutrient loadings, lake nutrients, and water clarity. Pages 69–96 in J. F. Kitchell, editor. *Food web management: a case study of Lake Mendota*, Wisconsin. Springer-Verlag, New York.
- Lathrop, R. C. 1992b. Benthic macroinvertebrates. Pages 173–192 in J. F. Kitchell, editor. *Food web management: a case study of Lake Mendota*, Wisconsin. Springer-Verlag, New York.
- Latta, W. C. 1938. *Outline history of Indiana agriculture*. Epsilon Sigma Pi and Purdue University, West Lafayette, Ind. 372 pp.
- Lee, R. G., R. O. Flamm, M. G. Turner, C. Bledsoe, P. Chandler, 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.
- Leopold, L. 1990. Ethos, equity and the water resource. *Environment* 32:16–20.
- Litvaitis, J. A. 1993. Response of early successional vertebrates to historic changes in land use. *Conservation Biology* 7:866–873.
- Lorimer, C. G. 1985. The role of fire in the perpetuation of oak forests. Pages 8–25 in J. E. Johnson, editor. *Proceedings of a symposium on challenges in oak management and utilization*. Madison, Wisconsin, 28–29 March 1985. WEX Cooperative Extension Service, University of Wisconsin Extension, Madison.
- Lynch, J. F., and D. R. Whigham. 1984. Effect of forest fragmentation on breeding bird communities in Maryland, U.S.A. *Conservation Biology* 28:287–324.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.
- MacLeish, W. H. 1994. *The day before America*. Houghton Mifflin, Boston. 277 pp.
- Mader, H. J. 1984. Animal habitat isolation by roads and agricultural fields. *Biological Conservation* 29:81–96.
- Magnuson, J. J., and R. C. Lathrop. 1992. Historical changes in the fish community. Pages 193–232 in J. F. Kitchell, editor. *Food web management: a case study of Lake Mendota, Wisconsin*. Springer-Verlag, New York.
- Margules, C. R., G. A. Milkovits, and G. T. Smith. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonium squama* and an amphipod. *Ecology* 75:2033–2042.
- Master, L. 1990. The imperiled status of North American aquatic animals. *Biodiversity Network News* 3:5–7.
- McCabe, R. E., and T. R. McCabe. 1984. Of slings and arrows: an historical perspective. Pages 19–72 in L. K. Halls, editor. *White-tailed deer ecology and management*. Stackpole Books, Harrisburg, Pa.
- McCoy, E. D., and H. R. Mushinsky. 1994. Effects of fragmentation on the richness of vertebrates in the Florida scrub habitat. *Ecology* 75:446–457.
- McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries: effects of roads on behavior, habitat use and demography. *Journal of Applied Ecology* 25:451–460.
- McShea, W. J., and J. H. Rappole. 1992. White-tailed deer as a keystone species within forested habitats of Virginia. *Virginia Journal of Science* 43:177–186.
- Meyer, W. B. 1995. Past and present land use and land cover in the USA. *Consequences*, Spring 1995:25–33.
- Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. *Fisheries* 14:22–38.
- Miller, S. G., P. Bratton, and J. Hadigan. 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. *Natural Areas Journal* 12:67–75.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* 9:279–294.
- Mladenoff, D. J., M. A. White, J. Pastor, and T. R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3:294–306.
- Mooney, H. A., editor. 1996. *Functional roles of biodiversity: a global perspective*. John Wiley & Sons, New York. 493 pp.
- Morrison, P. H., D. Kloepfer, D. A. Leverage, C. M. Socha, and D. L. Ferber. 1991. *Ancient forests in the Pacific Northwest: analysis and maps of twelve national forests*. Wilderness Society, Washington, D.C. 13 pp. + 10 maps.
- 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. 165 pp.
- National Research Council. 1992. *Restoration of aquatic ecosystems: science, technology, and public policy*. National Academy Press, Washington, D.C. 552 pp.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16:4–21.
- Nelson, E. W. 1876. Birds of northeastern Illinois. *Bulletin of the Essex Institute* 8:89–155.
- Nichols, S. A., R. C. Lathrop, and S. R. Carpenter. 1992. Long-term vegetation trends: a history. Pages 151–172 in J. F. Kitchell, editor. *Food web management: a case study of Lake Mendota, Wisconsin*. Springer-Verlag, New York.
- Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Natural Areas Journal* 9:211–213.
- 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, Inc., Sunderland, Mass.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. *Endangered ecosystems of the United States: a preliminary assessment of loss and degradation*. National Biological Service Biological Report 28. 58 pp.
- Nyland, R. D., W. C. Zipperer, and D. B. Hill. 1986. The development of forest islands in exurban central New York State. *Landscape and Urban Planning* 13:111–123.
- Osborne, L. L., and D. A. Kovacic. 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology* 29:243–258.
- Parker, G. R. 1991. History and management of central hardwood forests. Pages 20–25 in D. C. Le Master and G. R. Parker, editors. *Ecosystem management in a dynamic society*. *Proceedings of a conference*, Department of Forestry and Natural Resources, Purdue University, West Lafayette, Ind.
- Parker, G. R., and J. E. Van Kley. 1993. Brown County State Park: final report on vegetation damage by white-tailed deer. Report to the Division of State Parks, Indiana Department of Natural Resources.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* 8:17–26.
- Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecology* 8:3–18.
- Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. *Conservation Biology* 7:363–370.
- Porneluzi, P., J. C. Bednarz, L. J. Goodrich, N. Zawada, and J. Hoover. 1993. Reproductive performance of territorial ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. *Conservation Biology* 7:618–622.
- Powell, D. S., J. L. Faulkner, D. R. Darr, Z. Zhu, and D. W. MacCleery. 1993. *Forest resources of the United States, 1992*. U.S. Forest Service General Technical Report RM-234. 132 pp.
- Rasmussen, W. D. 1974. *American agriculture: a short history*. U.S. Department of Agriculture, Economic Research Service, Washington, D.C.
- Reeves, M. C. 1976. *Wildlife and its management in Indiana from 1716–1900*. Pages 2–4 in H. E. McReynolds, editor. *Fish and wildlife in Indiana, 1776–1976*. *Proceedings of the American Fisheries Society and The Wildlife Society*.
- Reice, S. R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist* 82:424–435.
- Ricker, W. E. 1963. Big effects from small causes: two examples from fish population dynamics. *Journal of Fisheries Research Board of Canada* 20:257–264.
- Ridgway, R. 1873. The prairie birds of southern Illinois. *American Naturalist* 7:197–203.
- Ridgway, R. 1889. *The ornithology of Illinois*. Volume 1. Illinois State Laboratory of Natural History. 520 pp.
- Ridgway, R. 1895. *The ornithology of Illinois*. Volume 2. Illinois State Laboratory of Natural History. 202 pp.
- Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* 257:524–526.
- Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408–418 in J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of Neotropical migrant landbirds*. Manomet Bird Observatory, Manomet, Mass.
- Robinson, S. K., J. A. Grzybowski, S. I. Rothstein, M. C. Brittingham, L. J. Petit, and F. R. Thompson. 1993. Management

- implications of cowbird parasitism on Neotropical migrant songbirds. Pages 93–102 in D. M. Finch and P. W. Stangel, editors. Status and management of Neotropical migratory birds. U.S. Forest Service General Technical Report RM-229.
- Rothstein, S. I., J. Verner, and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic brown-headed cowbird. *Ecology* 65:77–88.
- Rouse, C. 1986. Fire effects in northeastern forests: oak. U.S. Forest Service General Technical Report NC-105. 7 pp.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18–32.
- Schlesinger, R. C. 1989. Dynamics of the sugar maple component of a white oak–yellow poplar community. Pages 262–266 in G. Rink and C. A. Budelsky, editors. Proceedings of the fifth central hardwood conference. U.S. Forest Service General Technical Report NC-132.
- Schmelz, D. V., J. D. Barton, and A. A. Lindsey. 1975. Donaldson's Woods: two decades of change. Proceedings of the Indiana Academy of Science 84:234–243.
- Schulze, D., and H. A. Mooney, editors. 1993. Biodiversity and ecosystem function. Springer-Verlag, New York. 525 pp.
- Sedell, J. R., and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, U.S.A., from its floodplain by snagging and streamside forest removal. *Verhandlungen des Internationalen Vereins der Limnologie* 22:1828–1834.
- Simberloff, D. 1987. The spotted owl fracas: mixing academic, applied, and political ecology. *Ecology* 68:766–772.
- Smith, B. E., P. L. Marks, and S. Gardescu. 1993. Two hundred years of forest cover changes in Tompkins County, New York. *Bulletin of the Torrey Botanical Club* 120:229–247.
- Smith, R. J., and J. M. Schaefer. 1992. Avian characteristics of an urban riparian strip corridor. *Wilson Bulletin* 104:732–738.
- 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*. In press.
- Steffen, J. F. 1985. Some effects of clearcutting on songbird populations in the northern hardwood forest. *Wisconsin Academy of Science, Arts, and Letters* 73:123–132.
- Stewart, O. C. 1956. Fire and the first great source employed by man. Pages 115–184 in W. L. Thomas, editor. *Man's role in changing the face of the earth*. University of Chicago Press, Ill.
- Swift, B. L. 1974. Status of riparian ecosystems in the United States. *Water Resource Bulletin* 20:223–228.
- Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571–573.
- Thompson, F. R., III. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. *Conservation Biology* 7:325–333.
- Thompson, F. R., III. 1994. Temporal and spatial patterns of breeding brown-headed cowbirds in the midwestern United States. *Auk* 111:979–990.
- Thompson, F. R., III, and E. K. Fritzell. 1990. Bird densities and diversity in clearcut and mature oak–hickory forest. U.S. Forest Service Research Paper NC-293. 7 pp.
- Thompson, F. R., III, J. R. Probst, and M. G. Raphael. 1993. Silvicultural options for Neotropical migratory birds. Pages 353–362 in D. M. Finch and P. W. Stangel, editors. Status and management of Neotropical migratory birds. U.S. Forest Service General Technical Report RM-229.
- Thompson, F. R., III, S. K. Robinson, T. M. Donovan, J. Faaborg, and D. R. Larsen. 1996. Biogeographic, landscape, and local factors affecting cowbird abundance and host parasitism levels. T. Cook, S. K. Robinson, S. I. Rothstein, J. N. Smith, and S. G. Sealy, editors. *In Ecology and management of cowbirds*. University of Texas Press, Austin. In press.
- Tilghman, N. G. 1987. Characteristics of urban woodlands affecting winter bird diversity and abundance. *Forest Ecology and Management* 21:163–175.
- Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53:524–532.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* 367:363–365.
- Turner, M. G. 1987. Land-use changes and net primary production in the Georgia, U.S.A., landscape: 1935–1982. *Environmental Management* 11:237–247.
- Turner, M. G. 1990. Landscape changes in nine rural counties in Georgia, USA. *Photogrammetric Engineering and Remote Sensing* 56:379–386.
- Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit animal models in land management. *Ecological Applications* 5:12–16.
- Turner, M. G., D. N. Wear, and R. O. Flamm. 1996. Influence of land ownership on land-cover change in the southern Appalachian highlands and Olympic Peninsula. *Ecological Applications*. In press.
- Ubelaker, D. 1988. North American Indian population size, A.D. 1500–1985. *American Journal of Physical Anthropology* 77:289–294.
- Van Lear, D. H., and T. A. Waldrop. 1989. History, uses, and effects of fire in the Appalachians. U.S. Forest Service General Technical Report SE-54. 20 pp.
- Villard, M.-A., P. R. Martin, and C. G. Drummond. 1993. Habitat success and pairing success in the ovenbird (*Seiurus aurocapillus*). *Auk* 110:759–768.
- Wallin, D. O., F. J. Swanson, and B. J. 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.
- Wauters, L., P. Casale, and A. A. Dhondt. 1994. Space use and dispersal of red squirrels in fragmented habitats. *Oikos* 69:140–146.
- 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(4):1173–1188.
- Weaver, J. E., and F. E. Clements. 1938. *Plant ecology*. McGraw Hill, New York. 601 pp.
- West, N. E. 1993. Biodiversity of rangelands. *Journal of Range Management* 46:2–13.
- Whitcomb, R. F., J. F. Lynch, M. K. Klimkiewicz, C. S. Robbins, B. L. Whitcomb, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125–205 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- White, D. W., W. Worthen, and E. W. Stiles. 1990. Woodlands in a post-agricultural landscape in New Jersey. *Bulletin of the Torrey Botanical Club* 117:256–265.
- White, M. A., and D. J. Mladenoff. 1994. Old-growth forest landscape transitions from pre-European settlement to present. *Landscape Ecology* 9:191–205.
- White, P. S., and S. P. Bratton. 1980. After preservation: philosophical and practical problems of change. *Biological Conservation* 18:241–255.
- Whitney, G. G. 1994. From coastal wilderness to fruited plain: a history of environmental change in temperate North America, 1500 to present. Cambridge University Press, Cambridge, England. 451 pp.
- Williams, M. 1989. *Americans and their forests: a historical geography*. Cambridge University Press, New York. 599 pp.
- Wissmar, R. C., J. E. Smith, B. A. McIntosh, H. W. Li, G. H. Reeves, and J. R. Sedell. 1994. A history of resource use and disturbance in riverine basins of eastern Oregon and Washington (early 1800's–1990's). *Northwest Science* 68, Special Issue:1–35.
- Witham, J. W., and M. L. Hunter, Jr. 1992. Population trends of Neotropical migrant landbirds in northern coastal New England. Pages 85–95 in J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of Neotropical migratory*

- landbirds. Smithsonian Institution Press, Washington, D.C.
- Witmer, G. W., and D. S. deCalesta. 1992. The need and difficulty of bringing the Pennsylvania deer herd under control. *Proceedings of the Eastern Wildlife Damage Control Conference* 5:130–137.
- Wyckoff, W., and K. Hansen. 1991. Settlement, livestock grazing and environmental change in southwest Montana, 1860–1990. *Environmental History Review*, Winter:47–71.
- Yahner, R. H., and D. P. Scott. 1988. Effects of forest fragmentation on depredation of artificial nests. *Journal of Wildlife Management* 52:158–161.

Effects of Fire Suppression on Ecosystems and Diversity

- Agee, J. K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, D.C. 493 pp.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Covington, W. W., R. L. Everett, R. Steele, L. L. Irwin, T. A. Daer, and A. N. D. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. Pages 13–63 *in* R. N. Sampson and D. L. Adams, editors. *Assessing forest ecosystem health in the inland west*. Food Products Press. 461 pp.
- Fox, L., E. H. Biery, and J. D. Stuart. 1992. A technique to measure the effects of wildfire on landscape diversity, Klamath Mountains, California. Pages 158–162 *in* R. R. Harris and D. C. Erman, technical coordinators. *Proceedings of the symposium on biodiversity of northwestern California*. Report 29, Wildland Resources Center, University of California, Berkeley.
- Gruell, G. E., W. C. Schmit, S. F. Arno, and W. J. Reich. 1982. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana—implications for resource management. U.S. Forest Service General Technical Report INT-130. 42 pp.
- Hobbs, R. R., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324–337.
- Johnson, C. G., R. R. Clausnitzer, P. J. Mehringer, and C. D. Oliver. 1994. Biotic and abiotic processes of eastside ecosystems: the effects of management on plant and community ecology, and on stand and landscape vegetation dynamics. U.S. Forest Service General Technical Report PNW-GTR-322. 66 pp.
- Langston, N. 1995. *Forest dreams, forest nightmares: the paradox of old-growth in the inland West*. University of Washington Press, Seattle. 368 pp.
- Martin, R. E. 1982. Fire history and its role in succession. Pages 92–99 *in* J. E. Means, editor. *Proceedings of forest succession and stand development research in the Pacific Northwest*. Oregon State University, Corvallis.
- Martin, R. E., and D. B. Sapsis. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. Pages 150–157 *in* R. R. Harris and D. C. Erman, technical coordinators. *Proceedings of the symposium on biodiversity of northwestern California*. Report 29, Wildland Resources Center, University of California, Berkeley.
- Oliver, C. D. 1981. *Forest development in North America following major disturbances*. Forest Ecology and Management 3:153–168.
- Oliver, C. D., and B. C. Larson. 1990. *Forest stand dynamics*. McGraw-Hill, New York. 467 pp.
- Pyne, S. J. 1982. *Fire in America: a cultural history of wildland and rural fire*. Princeton University Press, N.J. 654 pp.
- Reice, S. R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist* 82:424–435.
- Romme, W. H., and D. G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience* 39:695–699.
- Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *Forest Science* 34:960–979.
- Schowalter, T. D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. *Canadian Journal of Forest Research* 19:318–322.
- Stuart, J. D., M. C. Grifantini, and L. Fox. 1993. Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, northwestern California. *Forest Science* 39:561–572.
- Whittaker, R. H. 1977. Evolution of species diversity in land communities. Pages 1–67 *in* M. K. Hecht, W. C. Steele, and B. Wallace, editors. *Evolutionary biology*. Volume 10. Plenum Press, New York.