Special Coverage:

CONSERVATION OF WOODY, EARLY SUCCESSIONAL HABITATS AND WILDLIFE IN THE EASTERN UNITED STATES

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Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats

by Robert A. Askins

etween 1750 and 1940, a wave of forest clearing swept across the eastern United States (Williams 1989, Pimm and Askins 1995). Its pace accelerated in the nineteenth century as settlers moved westward from the Atlantic coastal plain. The tall deciduous forests of the Ohio Valley were felled and burned to create farmland, and northern coniferous forests were converted to stumps and logging debris. In the late nineteenth century, large-scale timber harvesting shifted to the pine woodlands and bottomland hardwood forests of the Southeast. Only small woodlots remained in the wake of logging and settlement in many parts of the East. Given this history of widespread forest clearing, it is not surprising that propagation of trees and protection of forests became almost synonymous with conservation in eastern North America. Wetlands received protection much later, and natural shrublands and grasslands (habitats that resembled the fields and pastures that had replaced the forests) were largely ignored.

One of the most dramatic examples of the low priority given to open habitats was the destruction of the Hempstead Plains of Long Island, a 20,000-ha little bluestem prairie with a great diversity of specialized grassland plants and birds (Askins 2000). Most of this grassland was developed in the 1940s and 1950s without notable opposition from conservation organizations or ecologists. By the 1960s, this bluestem prairie had been reduced to a 240-ha patch at Mitchel Field, a military airfield. After the airfield was decommissioned in 1968, conservation groups led by The Citizens for the Hempstead Plains were able to save only 2 tiny relict patches of native grassland (both less than 25 ha). Other open habitats, such as coastal scrublands, oak savannas, and pine savannas, have met a similar fate in virtually every region of eastern North America. Of the ecosystems in eastern North America that have declined by >98%, 55% are grassland, savanna, and barren communities and 24% are shrubland communities (Noss et al. 1995, Thompson and DeGraaf 2001). Even open habitats that have not been decimated to this extent have been greatly reduced. For example, >90% of the coastal heathlands of Long Island and New England and 69% of the pocosins (evergreen shrub bogs) of the southeastern coastal plain have been destroyed (Noss et al. 1995).

The identification of conservation with woodlands remained strong in eastern North America long after many of the forests had grown back. Forest now covers more than 81% of New England and 54% of the Middle Atlantic states (Trani et al. 2001). The amount of forest in these regions and in the Southeast has increased progressively since the late 1800s, primarily because of farm abandonment (Pimm and Askins 1995). As Williams (1989: 471) points out, although abandonment of farmland was one of the predominant patterns of land-use change in eastern North America during this period, it was largely ignored because it conflicted with notions of

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progress and the advance of civilization: "In a society imbued with the frontier ideals of development, progress, and the virtues of forest clearing, [farm] abandonment was retrogressive, difficult to comprehend, and even sinful to contemplate."

Many species that thrived during the period of farm abandonment because of the prevalence of abandoned pastures and old fields have subsequently declined to dangerously low levels (Askins 1998, Hunter et al. 2001). Many of these species are probably native to the eastern forest region, originally depending on open habitats that were widespread before European settlement (Hunter et al. 2001, Lorimer 2001). These species are in trouble not only because of the intensification of farming and declining numbers of pastures, hay meadows, and abandoned fields, but also because of the suppression of natural disturbances—fires, beaver (*Castor canadensis*) activity, and floods—that generate natural grasslands and shrublands.

Resource managers who are responsible for extensive wilderness areas can manage for early successional habitats in a straightforward way by permitting or re-introducing natural disturbances.

Certainly the loss of old-growth forests and the degradation and fragmentation of second-growth forests in eastern North America are major concerns, but another legitimate concern is the decline of early successional habitats dominated by grass, shrubs, or young trees. Frank Thompson, Richard DeGraaf, and Margaret Trani organized this special section to address this concern. The papers in this special issue demonstrate convincingly that without active management we will lose some of the most interesting and diverse natural communities in eastern North America.

Perceptions of beauty and conservation priorities

A major barrier to actively sustaining or restoring open habitats is the common perception that these habitats are uninteresting or even unappealing. This is less true of meadows and other grasslands, which are associated with wildflower displays and a diversity of conspicuous and colorful butterflies and birds. As Gobster (2001) points out, however, shrublands and young forests are typically closed and monotonous, without the open views and coherent patterns that people generally prefer in landscapes. Compounding this problem, most of the animals associated with shrublands are reclusive and well hidden, so only experienced hunters and birders are likely to seek out these habitats to find animals (Gobster 2001). In addition, many contemporary shrublands and regenerating forests are produced by activities that conservationists often oppose. Species that depend on low, woody vegetation tend to be concentrated in powerline corridors, abandoned pastures, and clearcuts. In preserved areas, maintaining shrubland habitat is frequently controversial because it requires removing trees to favor vegetation associated with human disturbance.

Regional variation in shrubland declines

Trani et al. (2001) present a thorough analysis of trends in abundance of early successional woody habitats in different regions of eastern North America. The percentage of timberland in the "seedling–sapling" stage (areas dominated by young trees <12.7 cm in diameter) ranges from 16% in the Northeast to 32% in the coastal Southeast. The amount of young, regenerating forest has declined steadily in regions such as southern New England and the Middle Atlantic states, where the rate of farm abandonment has slowed in recent decades and where large-scale timber harvesting is infrequent. As Trani et al. (2001) point out, however, young woody vegetation is widespread in Maine and the Great Lakes states because of forest harvesting and in Ohio because of recent abandonment of farmland. Hence, trends in the availability of early successional habitat vary greatly in different regions.

Not surprisingly, some of the most severe declines in shrubland-dependent species have occurred in the Northeast (Witham and Hunter 1992, Askins 1993, Litvaitis 2001), where previously common shrubland specialists, such as New England cottontail (*Sylvilagus transitionalis*), golden-winged warbler (*Vermivora chrysoptera*), and yellow-breasted chat (*Icteria virens*), now appear on state lists of endangered and threatened species. In contrast, populations of some of the shrubland species associated with the boreal forests of Maine and the Great Lakes states, such as Nashville warbler (*Vermivora ruficapilla*) and Lincoln's sparrow (*Melospiza lincolnii*), have increased significantly in recent decades (Hunter et al. 2001), probably because they thrive in forest openings resulting from timber harvesting. Superficially, it would appear that shrubland species should show a similar pattern in the coastal Southeast because 35% of the timberland is in the seedling–sapling stage

(Trani et al. 2001), but many shrubland specialists are declining in this region (Krementz and Christie 2000). Many of the young forests in the Southeast are intensively managed pine plantations. Intensive timber management reduces the duration and diversity of the vegetation of low-stature, regenerating forest and consequently may diminish its value as habitat for early successional species of animals (Dickson et al. 1995, Hunter et al. 2001). We therefore need to be attuned to the different types of early successional habitat encompassed in the "seedling–sapling" and "non-stocked" categories in forest inventories.

Types of early successional, woody habitat

Lorimer (2001) makes an important distinction between "successional habitat" dominated by pioneer species and "young forest habitat" dominated by young stands of late successional species. Successional habitat occurs where plants colonize treeless areas created by river action, glaciation, or abandonment of cleared land. When people abandon farmland or beavers abandon impounded streams, the resulting old field or beaver meadow is eventually colonized by pioneer species of vines, shrubs, and trees (Figure 1, Thompson and DeGraaf 2001). In contrast, disruption or destruction of the forest canopy by fire, insect outbreaks, wind storms, or logging results in a young forest dominated by short sprouts and seedlings of mature forest trees, along with surviving shrubs and herbs from the original forest understory. Both types of habitat are dominated by low, woody vegetation, but they differ greatly in vegetation structure. Also, young forest habitats usually are more transitory than are early successional habitats because tree saplings and sprouts grow up quickly, spreading their crowns to form a closed canopy that shades out many plants in the herb and shrub layers (Thompson and DeGraaf 2001).

Figure 1. Successional habitat on an abandoned pasture in Connecticut. This habitat supports a diversity of shrubland species.

Although the animal communities of these 2 general types of low, woody habitat are similar, there are some differences. Successional habitats typically have a larger proportion of woody vines and shrubs than do young forest habitats, so they attract species that favor dense thickets. For example, in southeastern Connecticut, white-eyed vireos (*Vireo griseus*) were common in the dense early successional habitat on powerline rights-of-way, but were not found in clearcuts that were dominated by young forest (Askins 1990, Askins unpublished data). Other species are more frequently associated with young forests than with early successional, shrub-dominated thickets. For example, ruffed grouse (*Bonasa umbellus*) do best in young, even-age deciduous forests, particularly aspen forests (Dessecker and McAuley 2001). More intensive forestry practices (e.g., tree planting and herbicide spraying) result in faster tree growth and more homogeneous vegetation, exaggerating the distinctive features of young forests and probably making them even less favorable to species associated with early successional thickets. The distinction between early successional thickets and young forest has received little attention from researchers, but it may be a key consideration in regional conservation planning.

Another potential consideration is the size of patches of particular types of shrubland habitat (Hunter et al. 2001, Thompson and DeGraaf 2001). As Noss et al. (1995) point out, in some cases preservation of small representative patches of particular habitat types, what they call the "living museum approach," may not protect all of the species associated with the habitat because many species are sensitive to the negative edge effects and isolation associated with habitat fragmentation. How frequently this applies to shrubland specialists is not clear, however, because many of these species may be adapted to colonizing small disturbance patches in heavily forested landscapes. Many shrubland species occupy and nest successfully in small, isolated shrubland patches (Rudnicky and Hunter 1993, Krementz and Chrisite 2000, Litvaitis 2001). Other species, however, may need large areas of shrubland (Hagan et al. 1997, Litvaitis et al. 2001, Thompson and DeGraaf 2001). Also, in regions with dense white-tailed deer (*Odocoileus virginianus*) populations, large openings may help reduce the impact of heavy browsing on the plant species composition of regenerating forest because deer tend to forage near the forest edge (Litvaitis 2001).

Hunter et al. (2001) emphasize another important consideration for conservationists that has received relatively little attention: the group of species that are not normally found in large openings but instead depend on small openings (canopy gaps) in the forest. These canopy-gap species are typically associated with mature forest, but they depend on disruption of the canopy to produce patches of low, dense vegetation. For example, Hunter et al. (2001) classify the cerulean warbler (*Dendroica cerulea*), a species known to depend on large expanses of mature forest (Robbins et al. 1992), as a disturbance-dependent species because it is usually found near openings adjacent to tall trees. Openings of this sort are particularly frequent in old-growth forests, where the collapse of a single gigantic tree can tear a sizable hole in the forest canopy (Clebsch and Busing 1989).

Other mature forest species may depend on early successional habitats for cover or food at particular times of the year. Black bears (*Ursus americanus*) feed on forbs and berries in forest openings, but depend on acorns and other nuts found in mature forest during autumn (Litvaitis 2001). Forest openings also are used by fledgling and adult songbirds in late summer, following the breeding season (Pagen et al. 2000, Hunter et al. 2001).

How much disturbance is enough?

The immediate reason for the decline of many shrubland and grassland species is the decline of farming. Before open-field agriculture was introduced into eastern North America, however, these species depended on habitats created by natural disturbances. Suppression of these disturbances ultimately endangers many of these species. If natural grasslands and shrublands were still widely available, then early successional species would not be so dependent on old fields, powerlines, and clearcuts.

Before human settlement, extensive openings were created by fires, beavers, floods, and windstorms. In most contemporary forests, wildfires are suppressed, floodwaters are contained, and beavers have been trapped out or their effects on the environment have been tightly constrained. Even wind storms cause less damage to the forest canopy because most forests are young and densely stocked with trees, making them resistant to blowdowns (Hunter et al. 2001).

Restoration of natural landscapes requires the re-introduction or simulation of these disturbances. Often the goal is to approximate the proportion of each major habitat in the landscape at the time of European settlement. For some regions, initial land-survey data provide reasonable estimates of the percentage of land covered by different habitat types. Extensive agricultural clearing and burning were practiced by people for centuries before the arrival of European settlers, however, so it is not certain that the landscape patterns encountered by early surveyors reflected a natural disturbance regime. As Lorimer (2001) points out, it is usually difficult to determine whether openings resulted from anthropogenic or natural disturbances.

Another approach is to attempt to estimate the frequency of beaver meadows, wildfires, open floodplains, and blowdowns that would characterize a region without human activity. Information on the frequency of wind storms, lightning strikes, and floods, and on potential locations for beaver dams, could be used to model the natural pattern of disturbances, but as Lorimer (2001) emphasizes, the frequency of these disturbances has probably varied over time. Thompson and DeGraaf (2001) suggest that we can compensate for this by estimating the historic range of variation of different habitat types. This could encompass disturbance regimes before and after the period of extensive Native American agriculture and burning and during different climatic periods since the last glacial period. If each habitat type is kept within this historic range of variation, then we should be able to sustain species that depend on particular habitats.

At a minimum we should ensure that every habitat type is well enough represented to sustain viable populations of all native species. Given the strong evidence for the prevalence of open habitats in eastern North America, grassland and shrubland species should be considered native to a region unless there is historical evidence of a range expansion into the eastern forest region after forest clearing by Europeans. Evidence for an eastward range expansion exists for a few species, but not for most shrubland and grassland species (Askins 2000). Range expansion within the eastern forest region, such as the northward extension of the range of the golden-winged warbler (Confer 1992), should not be an issue, however, because disturbance-dependent species have probably always shifted their distributions from region to region in response to the availability of ephemeral habitat created by major disturbances. For conservation purposes, these species should be considered native unless the historical evidence clearly indicates otherwise. This should replace the common (but often implicit) assumption that grassland and shrubland species are interlopers to the eastern forest region that do not warrant much conservation concern.

Emphasizing historic ranges of variability and population viability for early successional species should provide the minimum amount of habitat needed. This will require careful regional planning to balance the needs of these species with other conservation needs (Thompson and DeGraaf 2001).

Managing shrubland habitats

These insights about the habitat needs of disturbance-dependent species indicate that there is no single prescription to manage low, woody habitat. Some species are favored by the dense shrubland on powerline corridors and in beaver meadows. Other species benefit more from the dense growth of small trees in clearcuts and blowdowns. Still other species depend on the small canopy gaps in group selection cuts and tree falls. All of these types of habitat should be available in a region to sustain the full range of native species. Except in regions with immense wilderness preserves, this goal cannot be achieved without coordination by land managers in different nature preserves, wildlife refuges, parks, public forests, and private forests across a region (Thompson and DeGraaf 2001).

Resource managers who are responsible for extensive wilderness areas can manage for early successional habitats in a straightforward way by permitting or re-introducing natural disturbances. The ecological role of wildfires in many natural ecosystems is now widely recognized. Beavers can be allowed to modify the landscape in areas where roads, buildings, and fields will not be flooded. As forests mature, large and small blowdowns should become more frequent. Studying the impact of these natural disturbances can tell us a lot about the habitat requirements of early successional species. In managed forests, timber harvests can be designed to produce favorable habitat for some early successional species.

In wildlife management areas and nature preserves, stable shrublands can be created by selectively removing trees to favor shrubs. This method has been used successfully by utility companies for several decades to maintain relatively stable shrubland communities on powerline corridors (Askins 1998, Thompson and DeGraaf 2001). By favoring some plant species and removing others, the edges of shrublands can be subtly modified to produce the depth and openness that often are missing from unmanaged shrubland habitats and to enhance the visibility of natural floral and fruiting displays (Figure 2, Niering 1975, Gobster 2001). As Gobster (2001:479) argues, it may be possible "to make some early successional landscapes more visually interesting and comfortable for people yet still maintain the importance and integrity of those landscapes for the wildlife and plant species that depend on them." This may be a first step in converting an ignored and even unpopular habitat into a valued resource that people are willing to protect and sustain.

Figure 2. Forest opening managed with naturalistic landscaping methods in the Connecticut College Arboretum. Fast-growing trees and other woody plants are selectively removed to create an attractive shrub community.

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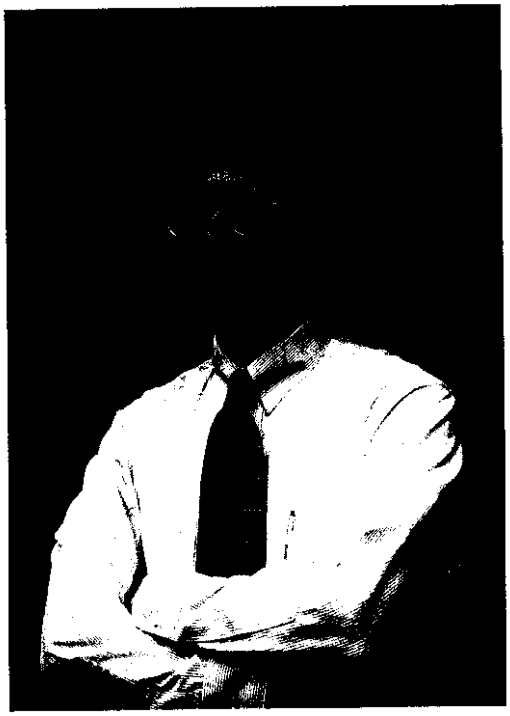

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Associate editors: *DeGraaf, Thompson, and Trani*

Patterns and trends of early successional forests in the eastern United States

by Margaret K. Trani, Robert T. Brooks, Thomas L. Schmidt, Victor A. Rudis, and Christine M. Gabbard

[illegible] the status of early successional forest conditions for 33 eastern states [illegible] New England, Middle Atlantic, Great Lakes, Central Plains, Coastal South, and Interior South subregions. We used Forest Inventory and Analysis surveys to analyze trends from 1946 to 1998. Dramatic regional differences occurred in distribution of early successional forests. The northeastern region had the least proportion of young forest (16%), followed by the north-central (24%) and southern (29%) regions. The least amount of young forest occurred in the Central Plains (15%) and New England (16%), whereas the greatest occurred in the pine-dominated Coastal South (32%). Differences also existed among individual states, ranging from 3% (Illinois) to 38% (Alabama). Long-term declines also were evident within the northeastern and north-central regions. Selective harvesting, fire suppression, urban sprawl, and cessation of agricultural abandonment contributed to the present imbalance in distribution of young forests. Private ownership predominates in the East and presents a significant challenge to provide young forests. Absence of proactive management on private lands may promote continued declines in early successional forest within many eastern areas.

Key Words early successional forest, eastern forests, forest ownership, land-use change

he status and trends of early successional forest and associated wildlife species have emerged as a concern within the eastern United States (Askins et al. 1990, Droege 1998, Litvaitis 2001). Early successional habitats are an integral component of the landscape. Young forests are ephemeral, changing with forest growth and succession. These community types depend on repeated disturbance such as fire, storm, or timber harvest. Within the last several decades, there have been significant changes in disturbance patterns of these forests (Lorimer 2001).

The forests of the eastern United States provide an important environment for a diversity of species (Porter and Hill 1998). Nationwide estimates indicate that approximately 80–90% of vertebrate species rely on forests for part of their life requirements (Flather and Hoekstra 1989).

Eastern forests have developed in response to a complex array of processes. Prior to European settlement, natural disturbances (e.g., wildfire, wind, and storms) enabled the maintenance of early successional forests

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(Williams 1989, Lorimer 2001). In addition, Native Americans frequently burned forest areas to maintain open woods dominated by herbaceous vegetation, facilitating agricultural conversion and game hunting (Whitney 1994). European settlement resulted in extensive clearing of forest and conversion of the land to pasture or cropland (DeGraaf and Miller 1996). These lands were often managed with fire, which also was used to maintain savannas and other open areas in the East (Williams 1989). In particular, fire was used to create favorable grazing conditions for domestic animals (Healy 1985).

Providing young forests contributes to the biological diversity of the forested landscape. The continued maturation of timberland in eastern forests will contribute to the decline and potential loss of some of these species.

Today, fire suppression has allowed these areas to develop into forest. Forest land in many areas also has increased in the last century because of farm abandonment and recolonization by second-growth forests. As forests age, concerns related to seral structure and species composition are being raised (DeGraaf and Miller 1996). The distribution and abundance of young forests directly affects foraging and nesting opportunities for a variety of species.

Recent reports indicate that a number of early successional species are declining (Oliver and Larson 1996, Thompson and Dessecker 1997), including Bachman's sparrow (*Aimophila aestivalis*), Henslow's sparrow (*Ammodramus henslowii*), northern bobwhite (*Colinus virginianus*), prairie warbler (*Dendroica discolor*), blue-winged warbler (*Vermivora pinus*), New England cottontail (*Sylvilagus transitionalis*), and bobcat (*Lynx rufus*). Population declines of woodcock (*Philohela minor*) have been attributed to habitat loss and maturing of the nation's forests (McAuley and Clugston 1998). In addition, Probst and Weinrich (1993) found that declines in early successional avifauna have paralleled changes in land use as natural succession occurs. Fire suppression has substantially reduced the amount of young forest habitat available to wildlife.

We assessed early successional forest conditions for 33 eastern states. We present the current distribution, status, and ownership of young forest communities within a regional ecological context. We review temporal trends in abundance of young forest over a 6-decade interval and reference factors that have contributed to those trends. Finally, we discuss continuing concerns and the future outlook for young forests in the East.

Methods

We analyzed 3 major regions of the eastern United States. The northeastern region included the New England (Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, Vermont) and the Middle Atlantic (Delaware, Maryland, New Jersey, New York, Ohio, Pennsylvania, West Virginia) subregions. The north-central region included the Great Lakes (Michigan, Minnesota, and Wisconsin) and the Central Plains (Illinois, Indiana, Iowa, and Missouri) subregions. The southern region was divided into the Coastal South (Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Texas, Virginia) and the Interior South (Arkansas, Kentucky, Oklahoma, Tennessee) subregions.

Forest resource data came from surveys conducted by the United States Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis (FIA) between 1946 and 1998 (Table 1). FIA surveys, conducted on a periodic basis, report forest conditions based on the measurement and analysis of 0.4-ha plots stratified by county and state. Fixed-radius and variable-radius prism points select trees for measurement; area expansion factors are then assigned to each ground plot. These factors are used to extrapolate plot values from a per-acre basis to a population basis (i.e., an area expansion factor is basically the area that the plot represents for estimation purposes). These measurements form the basis of the FIA Eastwide Database (Hansen et al. 1992).

Ground plots are assigned to land-use classes using aerial photography and field sampling. Classes are established based on forest type, volume, age, size, density, or other parameters. Forest land was defined as land with 10% or more tree crown cover by trees of any size. Forest land was further classified into timberland for those areas capable of producing industrial wood at an annual rate greater than 1.4 m^3/hectare. Timberland does not include forests reserved from timber production, such as national parks and wilderness areas.

Inferences about changes in early successional habitat were made using stand-size class. Stand size is a structural classification based on predominant tree size and was used as a surrogate for stand age and development stage. Four classes are generally recognized: seedling–sapling (young successional stands with trees predominantly less than 12.7 cm diameter and at least 30.5 cm in high), poletimber (mid-successional stands between 12.7 cm and 27.9 cm diameter), and sawtimber (mid- to late successional stands greater than 27.9 cm diameter). Nonstocked is an additional category and refers to timberland with less than 10% stocking with growing tree species (e.g., recent cutover areas and reverting agricultural fields).

We charted historical trends using seedling–sapling and nonstocked acreage to minimize definition differences among survey periods and FIA regions. Historical definitions of nonstocked forest have included variable aspects of seedling–sapling habitat. In the past, FIA surveys were conducted by state and summarized by region. Decadal summaries are influenced strongly by the portion of the region included. To mitigate this influence, graphical summaries were depicted as a temporal moving average encompassing surveys for years closest to midpoints needed to survey an entire region.

The National Forest Inventory and Analysis Program adheres to a national set of standards related to the accuracy of each inventory. These standards establish comparable information on forest resources across the country, with each state survey designed to meet sampling errors at the 67% confidence limit (one standard error). A 3% error per 404,700 ha (one million ac) of timberland is the maximum allowable sampling error for area estimates. We caution the reader against looking for small changes in forest area from information reported herein. The values used in preparing summaries are strongly affected by which states were surveyed, changes in analytical methods, and variable definitions between surveys. Detailed information concerning the accuracy of state inventories can be obtained from each respective FIA research unit.

Results

Eastern distribution of young forests

The eastern United States accommodates an array of land uses and ecological communities. The distribution of early successional forest varies by climatic subzones with common broad vegetation patterns, termed ecological provinces (McNab and Avers 1994). Using the most recently available standardized data from FIA (Hansen et al. 1992), the proportion of timberland and seedling–sapling diameter class was presented by ecological province (Figures 1, 2).

In regions with most land in forest cover, most seedling–sapling frequency occurred in the "Mixed Forest" provinces, (i.e., forests dominated by a mixture of needle-leafed and broad-leafed species). A notable exception was the mountain region of northern New England. Among southern states, the Coastal South contained the greatest proportion of young forest. The proportion of seedling–sapling timberland was least in the mountain broadleaf forest-dominated areas of Kentucky, Tennessee, and northern Arkansas. Regions dominated by nonforest uses contain the least proportion, e.g., the eastern edge of Arkansas, western edge of Mississippi, and southern tip of Florida. Notable exceptions were the sparse forests of the western portion of east Texas and east Oklahoma, whose forests are disturbed periodically by occasional livestock grazing and other uses (Rudis 1998).

Among the northern states, most young forest occurred within the northern tier of the region (eastern Maine, northern Wisconsin, northeastern Minnesota, and western Michigan), followed by the agricultural-dominated broadleaf forest areas (Indiana, western Ohio, southern Illinois, and southern Wisconsin). Lesser frequencies

Table 1. Forest Inventory and Analysis data used in the present analysis by state and year of survey (1946–1998).

Subregion and state	Year of survey
Middle Atlantic	
Delaware	1986, 1972, 1957
Maryland	1986, 1976, 1964, 1950
New Jersey	1987, 1972, 1956
New York	1993, 1980, 1968, 1953
Ohio	1991, 1979, 1968, 1952
Pennsylvania	1989, 1978, 1965
West Virginia	1989, 1975, 1961, 1949
Central Plains	
Illinois	1998, 1985, 1962, 1948
Indiana	1998, 1986, 1967, 1950
Iowa	1990, 1974, 1957
Missouri	1989, 1972, 1959, 1947
Great Lakes	
Michigan	1993, 1980, 1966, 1955
Minnesota	1990, 1977, 1962, 1953
Wisconsin	1996, 1983, 1968, 1956
Interior South	
Arkansas	1995, 1988, 1978, 1969, 1959, 1953
Kentucky	1988, 1975, 1963, 1949
Oklahoma	1993, 1986, 1976, 1966, 1955
Tennessee	1989, 1980, 1971, 1961, 1948
New England	
Connecticut	1998, 1985, 1972, 1953
Maine	1995, 1982, 1971, 1959
Massachusetts	1998, 1985, 1972, 1953
New Hampshire	1997, 1983, 1973, 1960, 1948
Rhode Island	1998, 1985, 1972, 1953
Vermont	1997, 1983, 1973, 1966, 1948
Coastal South	
Alabama	1990, 1982, 1972, 1963, 1953
Florida	1995, 1987, 1980, 1970, 1959, 1949
Georgia	1997, 1989, 1982, 1972, 1961, 1953
Louisiana	1991, 1984, 1974, 1964, 1953
Mississippi	1994, 1987, 1977, 1967, 1957, 1946
North Carolina	1990, 1984, 1974, 1964, 1955
South Carolina	1993, 1986, 1978, 1968, 1958, 1947
Texas	1992, 1986, 1975, 1965, 1953
Virginia	1992, 1986, 1976, 1966, 1956

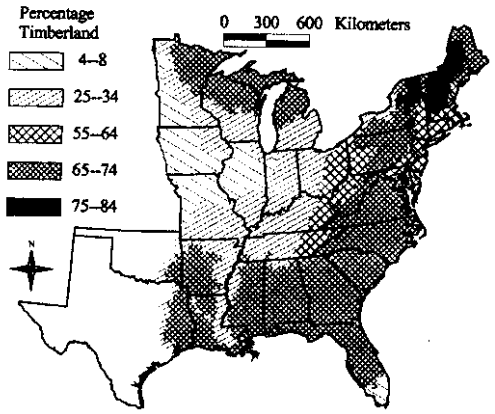

Figure 1. Percentage of eastern United States in timberland by ecological province, 1983–1998. Source: USDA Forest Service, Forest Inventory and Analysis Unit, Northeastern, North Central, and Southern Research Stations.

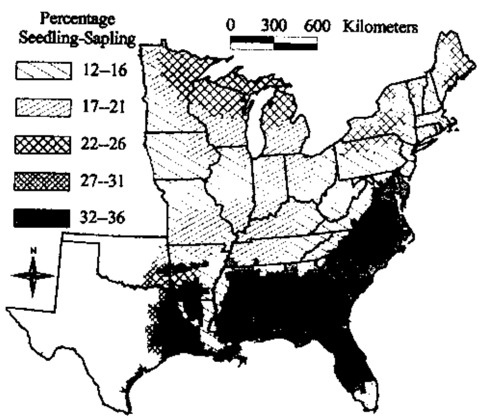

Figure 2. Percentage of timberland in the eastern United States in the seedling–sapling stand diameter class by ecological province, 1983–1998. Source: USDA Forest Service, Forest Inventory and Analysis Unit, Northeastern, North Central, and Southern Research Stations.

occurred in the mountain broadleaf forest-dominated mountains of eastern West Virginia and central Pennsylvania and the nonmountainous areas of southern New England, New Jersey, eastern Ohio, and western West Virginia. Least frequencies were in the agriculture-dominated areas of Iowa and northern Illinois and the mountain mixed forest-dominated areas of New York, New Hampshire, Vermont, and western Maine.

The status of young eastern forests: overview

Forest land comprised 40% (154 million ha) of the total land area within the eastern United States. Ninety-four percent (145 million ha) occurred as timberland encompassing a diversity of forest types. Forest types used herein reflect the species forming a plurality of live tree stocking based on the Society of American Foresters' Classification System (Eyre 1980). Oak–hickory (*Quercus–Carya*) forests were the predominant forest types within each region, occurring on approximately 52 million ha (Powell et al. 1993). On southern lands, oak–hickory has increased over 30% since the 1960s (Flather et al. 1999). Elm–ash–cottonwood (*Ulnus–Fraxinus–Populus*) forests also occurred throughout the eastern United States and were prevalent in bottomland and wetland areas. Northern hardwoods dominated the New England subregion, which also included white–jack–red pine (*Pinus strobus–Pinus banksiana–Pinus resinosa*) and spruce–fir (*Picea–Abies*) forests. Maple–beech–birch (*Acer–Fagus–Betula*) forests occurred on 20 million ha, predominantly in the northeastern and north-central regions. Over the last 4 decades, maple–beech–birch forests have increased over 40% in the North and South (Flather et al. 1999). Most aspen–birch (*Populus–Betula*) forests were located in the north-central region and consist of post-disturbance pioneer species. Aspen–birch forests have declined by 31% during the last 3 decades.

Forest composition in the South followed general ecological boundaries of the coastal plain and interior mountains. Loblolly–shortleaf pine (*Pinus taeda–Pinus echinata*) forests (20 million ha) occurred throughout the East, primarily in the South. This forest type has declined by 39% in the southern and by 13% in the northern United States since the 1960s. Longleaf–slash pine (*Pinus palustris–Pinus elliottii*) forests also have declined substantially (–45%) in the South during the last 4 decades (Flather et al. 1999). Oak–pine (*Quercus–Pinus*) forests occurred on 13 million ha and have increased throughout the East because of selective pine harvesting. Oak–gum–cypress (*Quercus–Nyssa–Taxodium*) forests were distributed over approximately 11 million ha; the extent of these hardwood forests has been reduced by 25% due primarily to agricultural conversion.

Within these eastern forests, most (67%) seedling–sapling timberland (24 million ha) was held in private ownership (e.g., individuals, corporations, and farmers). Private ownership included millions of small tracts. Industrial forests accounted for approximately 7 million ha (20%) of the seedling–sapling timberland. Companies and individuals operating wood-using plants own industry lands. The National Forest System managed 4% (1.6 million ha) of seedling–sapling timberland, whereas other

Table 2. Seedling–sapling distribution by primary ownership for timberland within the Northeastern United States, 1986–1998. Data provided in thousand hectares. (Source: USDA Forest Service, Northeastern Research Station, Forest Inventory and Analysis Unit).

				Seedling–Sapling Timberland					
State and Subregion	Survey year[a]	All land[b]	All timberland	Area	Percent[c]	National forest	Other public	Forest industry	Other private
Connecticut	1998	1,255	689	35	5	0	8[d]	0	27[d]
Maine	1995	7,994	6,855	1,706	25	0	27	861	818
Massachusetts	1998	2,030	1,055	47	4	0	8[d]	0	39[d]
New Hampshire[d]	1997	2,323	1,825	157	9	20	5	28	104
Rhode Island	1998	271	134	8	6	0	1[d]	0	7[d]
Vermont[e]	1997	2,396	1,814	178	10	5	6	15	153
New England		**16,269**	**12,372**	**2,131**	**17**	**24**	**55**	**904**	**1,148**
Delaware	1986	506	153	28	18	0	0	5	22
Maryland	1986	2,548	981	94	10	0	4	14	76
New Jersey	1987	1,922	754	101	13	0	23	0	78
New York	1993	12,231	6,235	1,028	16	0	40	33	954
Ohio	1991	10,607	3,063	733	24	6	17	14	696
Pennsylvania	1989	11,609	6,424	965	15	28	144	28	764
West Virginia	1989	6,238	4,823	486	10	23	8	36	419
Middle Atlantic		**45,661**	**22,433**	**3,435**	**15**	**57**	**236**	**130**	**3,009**
Northeastern Region		**61,930**	**34,805**	**5,566**	**16**	**82**	**291**	**1,034**	**4,157**

[a] N = 16,482 forested plots.
[b] From Powell et al. (1993).
[c] Percent of total timberland area.
[d] Area estimates based on relative density.
[e] Estimates of area calculated by ratio of total stand-size area estimated using basal area: total stand-size area using relative density.

public ownerships comprised almost 3 million ha (8%). These lands included military reservations, national parks, and wildlife refuges.

Urban areas, including transportation networks, have displayed substantial gains within all 3 regions. Urban growth rose by 24% in the South between 1982 and 1992 (USDA Natural Resource Conservation Service 1994). In the northeastern and north-central regions, urban areas increased by 13%.

There also have been substantial changes in forest composition and structure throughout the eastern United States during the past 6 decades. These are presented below by specific region.

Northeastern region

Forest land covered 38 million ha (67%) of the total land area within the 13 northeastern states as of the last national assessment (Powell et al. 1993). Forest land was the dominant land cover in New England, accounting for 81% of the total land area. In the Middle Atlantic, forest land covers 54% of the total land base. Timberland accounted for 93% (35 million ha) of forest land in the Northeast, 96% in New England, and 91% in the Middle Atlantic.

The forest resources of the Northeast were surveyed most recently by FIA from 1987 to 1998 (Table 2). At that time, seedling–sapling timberland comprised over 5 million ha (16%) of timberland. The proportion of timberland classified as seedling–sapling was equivalent for the 2 northeastern subregions, with New England having a slightly greater percentage (17%) than the Middle Atlantic (15%).

The proportion of timberland classed as seedling–sapling varies considerably by state, especially within New England. Maine, with considerable forest industry ownership (Birch 1996) and its associated active forest management, had the greatest proportion of timberland (25%) in the seedling–sapling class. The young forest component was dramatically less in the other New England states (e.g., Connecticut, Massachusetts, and Rhode Island). Seedling–sapling area in the Middle Atlantic ranged 10–24% of total timberland area. Ohio had the greatest proportion of young forest (24%) and reflected the active reversion of agricultural land into forest land, a phenomenon that occurred earlier in the eastern seaboard states.

Forest landownership was dominated by non-industrial private (NIPF) owners (Birch 1996). Except for Maine, seedling–sapling timberland was owned principally by individuals (Table 2). This has important implications for the use of timber harvesting for the retention of early successional forest land in the Northeast: 1) individual private forest landowners are resistant to using even-aged regeneration methods resulting in early seral stands, 2) NIPF owners are often interested in forest resources other than wood products and perceive timber harvest as detrimental to those interests, and 3) NIPF ownerships are increasingly fragmented into smaller tracts, impeding use of commercial harvest to manage forest resources

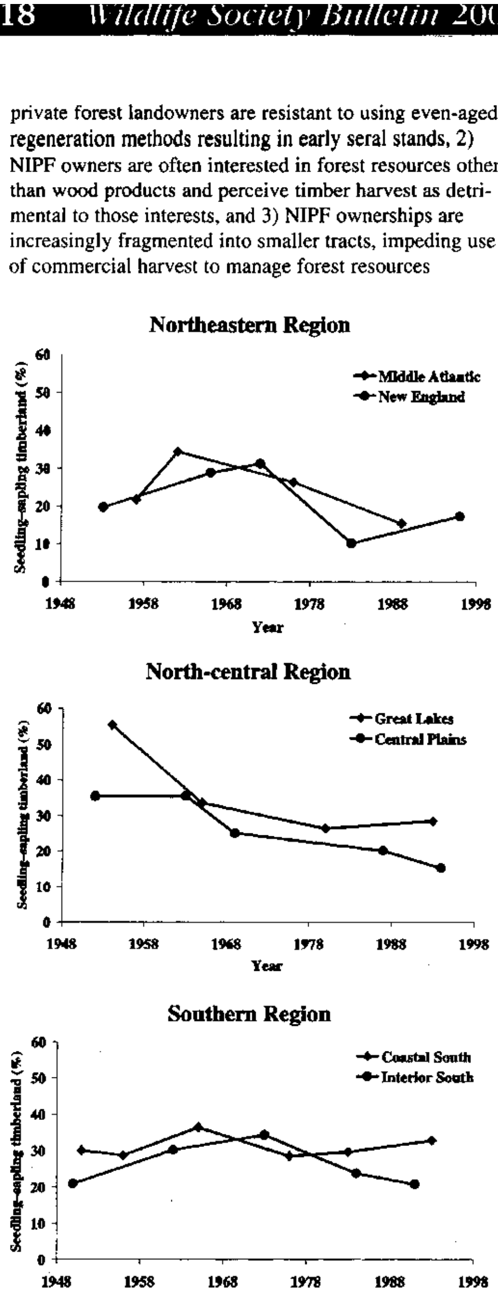

Figure 3. Temporal trends in seedling–sapling area for the eastern United States. Seedling sapling area is depicted as a percentage of total timberland area and includes nonstocked lands to minimize definition inconsistencies among survey periods. Source: USDA Forest Service, Forest Inventory and Analysis Unit.

(Brooks and Birch 1986, 1988; Kittredge et al. 1996).

Area of timberland in the Northeast increased by approximately 3.2 million ha between 1952 and 1987 (Alig et al. 1990). This occurred in the Middle Atlantic, with timberland area in New England remaining stable at 12.5 million ha. With the 1990s economic recovery and associated residential development, there has been an estimated timberland loss of 33,000 ha in New England. Projections of future development indicate declines (–1.6 million ha) in northeastern timberland over the next 4 decades (Alig et al. 1990).

Seedling–sapling availability within the New England and Middle Atlantic subregions peaked during the 1960–1970 period, followed by a decline that continues to the present day (Figure 3). However, the increase in seedling–sapling area observed in New England during the latest surveys reflects the influence of timber harvest occurring in Maine. Except for Maine, the area of seedling–sapling timberland in New England continued to decline in the 1990s. The forest surveys from the '90s showed that seedling–sapling timberland increased to 25% of total timberland in Maine, from 11.4% in the 1980s survey, but had declined to 7.9% from 8.6% in the other New England states.

The forest history of the Northeast since European settlement is one of relatively rapid and widespread change (DeGraaf and Miller 1996). There is no consensus about the full extent of Native American clearing of forest in the Northeast for agricultural purposes prior to the arrival of Europeans. However, there is agreement that agriculture was locally important along the Atlantic coast and along floodplains of major eastern rivers and that cleared areas, often maintained by fire, were extensive. Disease and conflict with Europeans decimated Native American numbers, resulting in the reforestation of the openings and shrub lands that had been maintained for agriculture and berry production.

European settlement resulted in the extensive clearing of forest and conversion of the land to pasture or cropland. In New England, it is estimated that forest land was most limited at about 1830, covering about 25% of the area (DeGraaf and Miller 1996). With the settlement of the Midwest, marginal farmland was abandoned in New England and reverted to forest cover. The abandonment accelerated following the Civil War, with federal government incentives for settlement of the western territories. The same pattern of land-use history occurred elsewhere in the Northeast, but at different dates and extent of forest loss.

The recent pattern of early successional forests across the Northeast reflects land-use change and forest succession occurring over the last 6 decades (DeGraaf and

Table 3. Seedling–sapling distribution by primary ownership for timberland within the north-central United States, 1989–1998. Data provided in thousand hectares. (Source: USDA Forest Service, North Central Research Station, Forest Inventory and Analysis Unit).

				Seedling–Sapling Timberland					
State and Subregion	Survey year[a]	All land[b]	All timberland	Area	Percent[c]	National forest	Other public	Forest industry	Other private
Illinois	1998	14,410	1,655	50	3	3	3	0	44
Indiana	1998	9,298	1,759	97	6	2	7	0	88
Iowa	1990	14,506	787	117	15	0	6	0	111
Missouri	1989	17,871	5,415	1,163	21	95	55	19	994
Central Plains		**56,085**	**9,616**	**1,427**	**15**	**100**	**71**	**19**	**1,237**
Michigan	1993	14,725	7,539	1,795	24	260	448	140	947
Minnesota	1990	20,619	5,963	1,800	30	234	795	131	640
Wisconsin	1996	14,078	6,360	1,953	31	158	491	178	1126
Great Lakes		**49,422**	**19,862**	**5,548**	**28**	**652**	**1,734**	**449**	**2,713**
North Central Region		**105,507**	**29,478**	**6,975**	**24**	**752**	**1,805**	**468**	**3,950**

[a] N = 33,424 forested plots.
[b] From Powell et al. (1993).
[c] Percent of total timberland area.

Miller 1996, Litvaitis et al. 1999). The period between the start of the Great Depression and the end of World War II was one of persistent agricultural abandonment. The loss of cropland and its reversion to forest was particularly evident in New England, where only 16% of the farms (and 37% of the croplands) that existed in 1945 remain today (Bureau of Census 1977, National Agricultural Statistics Service 1999). During the same period, 26% of the farms (and 70% of croplands) remain in the Middle Atlantic.

In the Northeast, abandoned agricultural land rapidly returns to forest cover. With the cessation of land abandonment and suppression of forest fires, creation of early successional forests originates from timber harvest and the occasional severe storm. However, extent of timber harvesting in the Northeast is limited, typically for intermediate silvicultural treatments (i.e., thinnings) and uneven-aged regeneration (Kittredge 1996). Neither harvest method results in creating adequate early successional forest habitat. The decline in forest products from the Northwest is occurring when northeastern forests are maturing to the stage where commercial operations are feasible. Within the constraints imposed by state regulations and ownership patterns, timber harvests may increasingly contribute to the retention of young forest.

North-central region

The Central Plains covered approximately 56 million ha of land. Seventeen percent was timberland, of which 15% occurred as young forest (Table 3, Brand and Walkowiak 1991, Hahn and Spencer 1991, Schmidt et al. 2000). In the past 15 years between FIA surveys, timberland has increased by 600,000 ha, whereas seedling–sapling timberland has declined by approximately 300,000 ha.

Most timberland was populated by deciduous species. Primary forest types in this region were oak–hickory, maple–beech–birch, and elm–ash–cottonwood. Depending on site factors, oak–hickory and maple–beech–birch forests were replacing early successional forests such as elm–ash–cottonwood.

Large-diameter trees dominated this subregion. Stand-size class distribution consisted of sawtimber (59%), poletimber (26%), and seedling–sapling (15%). In earlier surveys, 19% of the timberland area was classified as seedling–sapling (Figure 3). Selective harvesting methods that are generally used throughout the subregion often do not create the type of disturbance that can facilitate the creation of young forests. High-grading hardwood stands leaves lesser-quality cull trees that hasten the transition to a later seral stage.

Timberland ownership in the Central Plains was comprised of private and corporate landowners (85%), forest industry (3%), federal (7%), and state and local (6%). Two-thirds of all private landholdings were under 8 ha (Birch 1996). With expanding human population and timberland stabilization, forest resources in this subregion will continue to shrink in average tract sizes, which influences potential harvest and limits management options. In addition, only 1% of the landowners indicated that timber harvest was their primary reason for ownership (Birch 1996). It is projected that the current decline in area of early successional forest area will continue in this subregion.

Timberlands were predominantly on mesic sites. Less than 10% of the total area of timberland was on hydromesic (bottomland) sites of critical importance among a wide variety of interests. These bottomland hardwoods (or riparian forests) have historically received the most pressure for conversion to agricultural use. Current pressures included demands for urban space, second homes, and recreational facilities. Although trees often remain with development, forest characteristics change and natural regeneration is curtailed (Schmidt 2000). Stocking is lessened, snags and hollow trees are removed, and species composition is altered.

Prior to European settlement, the major disturbances in this region were flooding and wildfire. Windthrow has historically been of minor importance, with little impact on the forest resource. Bottomland sites of elm–ash–cottonwood were historically subjected to periodic floods. These disturbance events removed older stands and created riparian forests that were maintained in an early seral stage. Flood-control measures initiated over the past 50 years have caused a shift from early successional to mid-successional riparian forests throughout much of the Central Plains (Schmidt 2000). In addition, suppression of wildfires has promoted forest succession. Prior to European settlement, this region was exposed periodically to wildfires that maintained young forests and diverse species compositions. After World War II, expanded transportation networks and improved fire management resulted in dramatic wildfire declines (and thus minimal disturbance for early seral maintenance). The control of floods and fires, in combination with agricultural conversion, has greatly reduced the magnitude of forest disturbance (Schmidt et al. 2000). If this continues, seedling–sapling timberland will continue to decline over the next 2 decades.

The Great Lakes states covered approximately 49 million ha, 40% of which are classified as timberland (Table 3, Leatherberry et al. 1995, Schmidt et al. 1997, Schmidt 1998). Timberland has increased 1.3 million ha during the 1980–1993 survey period. This net increase in timberland area began in the 1970s from the conversion of agricultural lands and the reversion of "stumpland" areas (i.e., forest lands that have been cutover and left for natural regeneration to occur).

This subregion differed from the Central Plains relative to the proportion of young forest. Currently, 28% of total timberland exists as seedling–sapling stands. This contrasts with 25% in the 1980s, 28% in the 1960s, and 36% in the 1950s (Figure 3). There also have been dramatic shifts in nonstocked areas that comprised 19% in the 1950s and now cover less than 1% of current timberland.

Stand-size class distribution was relatively even within the Great Lakes subregion. Thirty-seven percent was classified as sawtimber, 35% as poletimber, and 28% as seedling–sapling. In the 1980s, 28% of the timberland area was classified as sawtimber, 46% poletimber, 25% seedling–sapling, and 1% nonstocked. This distribution is attributed to the harvesting techniques used in this subregion.

Coniferous and deciduous species occurred within this subregion. Dominant hardwoods included maple–beech–birch, oak–hickory, aspen–birch, and elm–ash–cottonwood. Depending on site factors, oak–hickory and maple–beech–birch forests replace undisturbed early successional forest types (i.e., elm–ash–cottonwood). With harvest, aspen–birch stands are self-replacing; without disturbance, these forests advance to mid-successional seres such as maple–beech–birch.

For many forest types, timber harvest creates a sufficient disturbance to allow regeneration of early successional species. For example, one method of harvesting aspen–birch stands is by using clearcutting techniques that ensure adequate regeneration and harvest efficiency. Selective hardwood harvesting methods (also used in the Northeast) do little to change successional stage.

The future levels of young forest depend greatly on which harvest techniques are used in the Great Lakes. Timberland was found on a variety of physiographic sites ranging from swamps and bogs to dry sandy plains; these sites are unlikely candidates for land-use conversion. Similar to other areas within the north-central region, former timberlands with agricultural potential have been converted, whereas flood and fire control have promoted forest expansion.

Forty-nine percent of seedling–sapling timberlands were in private ownership; 8% were managed by forest industry. National forests (12%) and other public agencies (31%) represent the remaining ownership sectors. Over 50% of private owners have less than 8 ha of timberland (Birch 1996). This region is a national vacation destination, with continual pressure for recreational cabins, second homes, and other recreational facilities. With the region's projected rise in population levels, current timberland resources may continue to become fragmented with reduced tract sizes. Development is currently the greatest land-use threat to the Great Lakes subregion.

Interior and Coastal South regions

Upland hardwoods dominated the Interior South, whereas a mixture of conifers and hardwoods populated the Coastal South. The South is bisected by the mountains (Georgia, Virginia, the Carolinas, Kentucky, and Tennessee) and by the Mississippi Alluvial Basin (Arkansas, Louisiana, and western Mississippi). Pine forests are concentrated on the coastal plain and on the

Table 4. Seedling–sapling distribution by primary ownership for timberland within the southern United States, 1988–1997. Data provided in thousand hectares. (Source: USDA Forest Service, Southern Research Station, Forest Inventory and Analysis Unit).

				Seedling–Sapling Timberland					
State and Subregion	Survey year[a]	All land[b]	All timberland	Area	Percent[c]	National forest	Other public	Forest industry	Other private
Illinois	1998	14,410	1,655	50	3	3	3	0	44
Arkansas	1995	13,488	7,443	1,768	24	97	55	505	1,111
Kentucky	1988	10,291	4,997	821	16	21	28	20	752
Oklahoma	1993	17,788	1,981	564	28	24	40	111	388
Tennessee	1989	10,676	5,368	947	18	22	41	116	768
Interior South		**52,243**	**19,789**	**4,100**	**21**	**164**	**164**	**752**	**3,019**
Alabama	1990	13,145	8,876	3,374	38	44	62	912	2,356
Florida	1995	13,986	5,929	2,190	37	141	187	813	1,049
Georgia	1997	15,001	9,630	3,298	34	34	87	805	2,374
Louisiana	1991	11,284	5,578	1,377	25	53	33	503	788
Mississippi	1994	12,151	7,522	2,831	38	87	67	553	2,125
North Carolina	1990	12,618	7,572	1,821	24	59	72	286	1,405
South Carolina	1993	7,799	5,040	1,805	36	64	44	377	1,321
Texas	1992	67,838	4,765	1,569	33	44	44	686	820
Virginia	1992	10,256	6,252	1,228	20	50	29	228	920
Coastal South		**164,078**	**61,164**	**19,493**	**32**	**576**	**625**	**5,163**	**13,158**
Southern Region		**216,321**	**80,953**	**23,593**	**29**	**740**	**789**	**5,915**	**16,177**

[a] $N = 49{,}137$ forested plots.

[b] From Powell et al. (1993).

[c] Percent of total timberland area.

piedmont. In the more productive areas of the South, the coastal plain has supported a "fourth" forest since the large-scale clearing of the late 1800s (USDA Forest Service 1988).

Dates of the most recent statewide surveys are between 1988 (Kentucky) and 1997 (Georgia). The regional composite of state surveys has an average survey date of 1992 (Table 4). Within the southern region, there were 216 million ha of land, 37% of which was timberland. Seedling–sapling stands accounted for 29% of the total timberland area.

The greatest proportion of young forest was in the Coastal South (32%). Alabama, Florida, Mississippi, and South Carolina each maintained over 35% of timberland in seedling–sapling. The Coastal South included approximately 10 million ha of plantations, 40% of the world's total (Hyde and Stuart 1998). The region's timber production continues to retain steady recruitment of young forest, largely in loblolly and slash pine plantations. Elsewhere, forests are succeeding to oak–pine, mixed hardwoods, and other late successional types (Rudis 1991). In the pine regions of the Gulf coastal plain, intensive plantation management has influenced forest composition and stage of stand development. Pine management was intensive in southwestern Alabama, southern Mississippi, southwestern Louisiana, southwestern Arkansas, southeastern Oklahoma, and southeastern Texas. The Ouachita Mountains of Arkansas and Oklahoma contain a large proportion of shortleaf pine and oak–pine community types.

In contrast, the Interior South contained 21% of timberland in seedling–sapling (Table 4). Within this subregion, Kentucky (16%) and Tennessee (18%) had the least amounts of seedling–sapling timberland; Arkansas (24%) and Oklahoma (28%) had the most. Recruitment of young forest has declined slowly in the Interior South (and other areas with few conifers).

Private ownership predominated in the South, as elsewhere. Sixty-nine percent of seedling–sapling timberlands were privately owned. Forest industry managed 25% of young forest timberland, largely in the Coastal South's pine-growing areas that were acquired during the Great Depression (Williams 1989). National forest (3%) and other public agencies (3%) represented the remaining ownership sectors within seedling–sapling timberland, located primarily in the mountain and lowland areas of the Coastal South (Rudis 1998).

Fire frequency and intensity were once dominant throughout the South. Effective fire suppression over the last 50 years has led to changes in forest ecosystems, including expansion of forest land within former open habitats (White and Wilds 1998). Tropical storms continue to provide recurrent disturbances in coastal areas, along with tornadoes in the interior. The heavy rainfall that accompanies these storms, an important natural disturbance, creates open areas within the forested landscape.

During the 1920s, southern forests consisted primarily of pines (*Pinus spp.*), oaks (*Quercus spp.*), cypress (*Taxodium Rich.*), tupelo (*Nyssa L.*), and sweetgum (*Liquidambar L.*). Presettlement fires and periodic droughts were the dominant ecological forces that gave rise to vast areas of southern pine forests (Williams 1989). In later decades, fire suppression and timber harvests, followed by land clearing for farm uses, reduced the extent of forest. However, a major period of farm abandonment occurred during the 1880–1940 period, with many old fields reverting initially to pine, which resulted in expanded areas of forest. During the following decades, forest area and early successional stand increases varied very little (Figure 3), with many of the losses balanced by gains elsewhere. Old-field natural pine types succeeded to upland hardwoods and older stands with time, fire suppression, and selective pine harvests. Pine plantation area has increased (Powell et al. 1993), particularly in the Coastal South.

In both portions, river bottom forests were drained and converted to cropland, notably in the Mississippi alluvial plain. Elsewhere, declines in forest land were the result of human settlement, animal agriculture, and urban uses (Healy 1985). Recent surveys indicate that net forest area has stabilized (McWilliams et al. 1997, Flather et al. 1999), with some of the stability due to incentive programs for private land reforestation.

By the 1990s, most forests in the Mississippi Alluvial Plain (71%), Central Appalachians (61%), and Eastern Broadleaf (57%) provinces were in the sawtimber-size class (Rudis 1998). Elsewhere, sawtimber-size class represented 30 to 45% of the forestland, with disturbances associated with forest fragmentation of nonforest cover (roads, agriculture, and urban land), and timber management activities the likely contributors to regional differences (Rudis 1998). Within subregions, localized prospects are less certain, as southern forests near urban developments and high population densities are tied to lesser harvest rates (Barlow et al. 1998). The South has become one of the nation's most rapidly growing areas, presenting an ever-increasing challenge to forest resource management.

Conclusion

There are dramatic regional differences in the distribution of early successional forests in the East. Sawtimber-sized trees currently dominate the northeastern and north-central regions. The proportion of timberland in young forest was smallest in the northeastern region (16%), followed by the north-central (24%) and southern (29%) regions. Within the Northeast, percentage of seedling–sapling forest remains relatively equal among the states comprising New England (17%) and the Middle Atlantic (15%). The proportion of seedling–sapling in the Great Lakes (28%) was almost double that in the Central Plains (15%) of the north-central region. The proportion of young forest in the Coastal South (32%) exceeds that found within the Interior South (21%). The distribution of young forest also varies considerably by state (Tables 2, 3, and 4).

The availability of seedling–sapling timberland in the East reflects the influence of land-use conversion, ownership, and minimal disturbance. Prior to European settlement, wildfires and other natural disturbances enabled maintenance of early successional forests (Lorimer 2001). Selective harvesting, effective fire suppression, and cessation of agricultural abandonment have contributed to the present distribution of young forests. The current distribution of young forest and of other shrubland habitats may be below that needed to sustain desired population levels of some wildlife and at the low range of historic conditions (Askins 2001, Thompson and DeGraaf 2001). The greatest concerns are in the Northeast and Central Plains. Concerns related to species composition and future condition also are being raised (McWilliams et al. 1997). Although forest area has increased in the North, the sites where this has occurred are often quite different from those sites where forest has been lost.

The magnitude of private ownership also presents a significant challenge for the provision of young eastern forests. Individual landowners are changing the characteristics of future forest resources. The absence of management on private lands may result in declines in early successional habitat within many eastern areas. Public agencies, including national forest systems, manage a very small proportion of available young forest in the East.

Urban areas have appreciably changed the character of the forested landscape. For example, urban land comprises a significant portion of the Northeast and has increased 53% during the 1960–1987 interval (Porter and Hill 1998). Population expansion also has resulted in ownership fragmentation. The small tracts typical of present land-use patterns provide little opportunity for forest management and natural disturbance sufficient to create early successional forest. This will continue to influence a myriad of wildlife species, positively for some species and negatively for others.

Wildlife species differ in their response to forest change and have unique preferences for forest characteristics. Many wildlife species rely on the seedling, shrub, and understory characteristics associated with younger stages. As the composition and structure of the forest change, so do the species that depend on these communities (DeGraaf 1991). There are several early successional species of management or conservation importance within eastern forests (Dessecker and McAuley 2001, Litvaitis 2001). Young forests provide quality habitats for many species, including several of conservation concern (Hunter et al. 2001). Other species use a variety of forest communities and seres. Providing young forests contributes to the biological diversity of the forested landscape. The continued maturation of timberland in eastern forests will contribute to the decline and potential loss of some of these species.

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Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change

by Craig G. Lorimer

Recent declines in habitat suitable for early successional wildlife species are interpreted in a broad historical context, using several types of scientific and historical evidence to estimate changes in amount of young forest habitat in presettlement and post-settlement eras. A major contrast in disturbance regimes between northern mesophytic hardwood forests and the oak-pine forests of the central and southern United States is evident for several thousand years before European contact. Catastrophic wind disturbance is a dominant feature in northern hardwood forests, but frequency is fairly low except in areas affected by Atlantic hurricanes. Most northern hardwood regions were dominated by old-growth forest in presettlement times, with young forest habitat (up to 15 years old) occupying <1% to 13% of the landscape in different states. In contrast, fire was a dominant force in shaping species composition and structure of oak-hickory and oak-pine forests, with savanna and grassland habitat occupying up to 65% of the landscape in some midwestern regions. Numerical estimates of the presettlement extent of young forest and savanna habitat are not possible for the Atlantic slope and Gulf regions, but the composition and structure of the vegetation seemed to bear the imprint of frequent fires in most areas where evidence is available. Comparison of historic fire frequency with modern lightning fire data suggests that humans caused most of these fires. Young forest habitat reached a peak of up to 55-60% of the forest cover in most states in the late nineteenth century because of logging, wildfires, fuelwood cutting, and farm abandonment, but has since declined to 20% or less in many regions.

Key Words anthropogenic fires, early successional habitat, historic disturbance frequency, natural disturbance, deciduous forests

ince the period of heavy exploitation in the early twentieth century, the eastern North American forest has been aging. Millions of hectares of forest considered to be "scrubby second growth" in the 1920s and '30s are now reaching maturity. In many areas, such as the Great Lakes region, changes in forest species composition also are occurring, with pioneer stands of aspen (*Populus* spp.), paper birch (*Betula papyrifera*), and oak (*Quercus* spp.) giving way to stands of maple (*Acer* spp.) and other late successional species (Whitney 1994, Schmidt 1997).

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While the trend toward mature and old-growth conditions will be beneficial for some wildlife species, it will create unfavorable conditions for others. For example, out of 126 species of Neotropical migrant songbirds in the northeastern U.S., 74 are considered to be largely dependent on early successional habitat and are typically scarce or absent in mature or old-growth forests (Smith et al. 1993). Although numerous factors, including tropical deforestation, fragmentation of temperate breeding grounds by human development, and brood parasitism, appear to be responsible for declines in some Neotropical migrant songbirds since the 1960s (Robbins et al. 1989, Terborgh 1992), simple maturation of the forest is likely an important factor for the early successional group (Hill and Hagan 1991, Litvaitis 1993). Seventy-six percent of the Neotropical migrants with declining population trends in the Northeast are classified as early successional species (Smith et al. 1993).

To some extent, recent declines in early successional species can be interpreted as a natural adjustment or recovery of the eastern North American forest from the cataclysmic and unprecedented levels of disturbance imposed by humans in the agrarian and industrial society of the late nineteenth and early twentieth centuries. The proportion of the land in early successional habitat was unusually high between 1890 and 1950 and population levels of associated wildlife species probably could not have been sustained at those levels without compromising other resource values. However, estimates concerning "baseline" or "normal" population levels of early successional animal species require detailed knowledge about historical disturbance regimes, and conclusions applicable to one area of the eastern forest might not be valid in another. For example, the amount of early successional habitat in the Boundary Waters region of Minnesota is currently less than in presettlement times because of effects of fire suppression (Frelich and Reich 1995). In the vast oak and pine regions of the central and southern U.S., historical evidence indicates that Native Americans created extensive open habitat by frequent intentional burning prior to European contact (Rostlund 1957, Whitney 1994). Regardless of historical levels of abundance, sufficient early successional habitat is needed to maintain viable populations of uncommon species that might potentially be at risk (Thompson et al. 1993).

Many ecologists believe that conservation of biological diversity in forests will require management plans that mimic to some extent the long-term historical and natural disturbance regime. The rationale is that management practices need to provide a similar mix of habitat conditions to which various organisms have become adapted to ensure their long-term survival (Seymour and Hunter 1999). The purpose of this paper is to synthesize existing knowledge on long-term changes in historical disturbance regimes for selected regions of eastern North America and to consider the specific question of historical fluctuations in amount of early successional habitat.

Because disturbance regimes are affected by long-term climatic change, and because animals became adapted to natural disturbance regimes over a period of many thousands of years, the discussion is not restricted to a simple "before-and-after" comparison of the forest immediately preceding European settlement with the forest in modern times. Rather, the discussion will include relevant paleoecological evidence from the Holocene, focusing especially on the past 9,000 years of the post-glacial period. This period comes after the widespread retreat of boreal spruce–pine forest and mass extinctions of Ice Age megafauna (De Graaf and Miller 1996), but includes the span of time when oak forest became distributed widely across the central U.S. (Watts 1979).

> [T]he question posed by Sprugel (1991:1), "What is 'natural' vegetation in a changing environment?" is one that managers must consider whenever they use information on past conditions to establish management goals.

Sources of evidence

Evidence on natural disturbance regimes and estimates of the proportion of the landscape in different forest age classes are derived from several independent lines of evidence. These include historical records, collection of modern scientific data from old stands, analysis of fossil pollen and charcoal from sediments, and direct observation of contemporary natural disturbances.

Each method produces unique information, but each also is subject to some interpretive ambiguities and site limitations. Not all methods can be used in every region of eastern North America because pertinent historical records may be lacking or suitable field sites may not be available. When all methods are used together, they can tell us a great deal about disturbance processes, frequency, and effects. Nevertheless, even when all methods are viewed together, quantitative estimates of the proportion of the landscape in early successional habitat are possible only for certain regions and for certain restricted periods of time.

General observations on disturbance frequency and pattern

Estimates of typical "baseline" values of early successional habitat should be interpreted cautiously because disturbance regimes can vary widely in time and space. Studies of disturbance patterns suggest the following guiding principles:

1) *Evidence on natural and anthropogenic disturbance is not disentangled easily.* Humans have occupied eastern North America for the past 12,000 years, essentially the entire post-glacial period (Delcourt et al. 1993). Evidence of fires may be present in sediment cores over much of this time, or as scars on trees in more recent centuries, but the relative importance of anthropogenic and natural fires can be inferred only from circumstantial, indirect evidence. The presence of maize pollen in nearby bogs or high levels of pollen of weedy, ruderal species suggests local occurrence of agricultural clearing (Delcourt 1987). Human influence also can be inferred from historical records of Native American village sites or archaeological evidence (Mathis and Crow 1983). In the Great Lakes region, Loope and Anderton (1998) and Dey and Guyette (2000) have used recent statistics on lightning fire frequency to interpret the proportion of fire scars in old forest remnants that might be attributable to natural versus human ignitions.

2) *Disturbance regimes vary over time.* Changes in global climate and air circulation patterns can have major effects on natural disturbance frequency. Increases in frequency of windstorms or droughts, for example, can lead to greater fire frequency (Clark 1990, Foster and Boose 1995). Past evidence of fluctuating disturbance regimes can be found in the pollen record. Clark (1990) demonstrated that fire frequency changed in concert with climatic fluctuations over a period of 750 years in Minnesota. Davis et al. (1998) reported a major change in forest composition and fire frequency in forests of northern Michigan about 3,000 years ago. Prior to that time, the forest was dominated by a woodland of white pine (*Pinus strobus*), oak, and red maple (*Acer rubrum*), and charcoal concentrations suggested reasonably frequent fires. After the invasion of hemlock (*Tsuga canadensis*) and mesic northern hardwoods about 3,000 years ago, charcoal deposition largely ceased. Incidence of fire use and land clearing by humans are likewise subject to wide fluctuations because of population shifts resulting from technological change (e.g., development of agriculture about 1,200 years ago), migration, disease, and warfare (Rostlund 1957, Delcourt et al. 1993, Dey and Guyette 2000). For these reasons, the natural and anthropogenic disturbance regime immediately preceding European settlement cannot necessarily be accepted as representative of a long-term baseline value.

In presettlement times, fire-maintained oak savannas occupied about 46 million hectares in the midwestern United States and were also common near rivers and native villages in the east coast and piedmont regions. This scene shows a prescribed burn in a restored oak savanna.

3) *Disturbance patterns on the landscape are spatially nonrandom.* Disturbances are dispersed neither uniformly nor randomly on the landscape, but are highly influenced by soil and topographic features and human settlement patterns. Examples include greater levels of hurricane damage on exposed versus sheltered slopes (Foster and Boose 1992), greater lightning fire frequency on exposed ridgetops (Delcourt and Delcourt 1998), greater fire frequency on sandy versus loamy soils (Whitney 1986), and greater disturbance by Native Americans near floodplains of major rivers (Delcourt 1987). Guyette and Dey (2000) demonstrated a significant correlation between fire frequency and topographic roughness of a landscape. The effect of all these patterns is to increase vegetative diversity at the landscape scale, which presumably enhances biological diversity. Another important consequence is that early successional habitat is not created randomly in space and time, but is more likely to be found on certain "dependable" habitats such as sandy outwash plains and upper south-facing slopes.

4) *Severe disturbance is highly episodic and spatially heterogeneous.* Rare but extensive natural disturbances can leave a long-lasting imprint on the landscape, but it is difficult to estimate their frequency. Catastrophic blowdown in the forests of northern Michigan has an estimated average natural rotation period of more than 1,500 years, but as is often the case with rare events, the standard error is even longer than the actual interval (Frelich and Lorimer 1991). Blowdown patches have ranged historically from 1 to 3,000 ha in most of the northern hardwoods region (Canham and Loucks 1984, Zhang et al.

Large blowdowns are a recurrent feature of the landscape in the northern hardwood region. Nineteenth century land surveyors recorded more than 400 blowdowns in northern Wisconsin alone. Average size was nearly 100 hectares. This scene shows the aftermath of a 1977 windstorm in a tract of old-growth forest on the Flambeau River State Forest, Wisconsin.

1999). But individual storms causing heavy damage on more than 50,000 ha have occurred in recent times in northern Wisconsin and northern New York (Dunn et al.1983, Folwell 1995). It is not known whether these "superstorms" are rare events of unknown frequency, or there has been a recent shift in the historic disturbance regime, or clusters of individual blowdowns in the land survey records were simply not recognized as having originated from single large storms. In regions with naturally low disturbance frequencies, the episodic nature of large natural disturbances creates a sort of "feast or famine" environment that may subject early successional animal populations to erratic fluctuations (see similar conclusions for the Yellowstone ecosystem by Romme and Knight 1982). Thus, the natural environment presents a much different situation from a managed forest on specified rotations, where timber harvest creates a dependable amount of young forest habitat annually.

Large disturbances such as crown fires or windstorms often undergo pulses of intensity which, when superimposed on a heterogeneous landscape, result in a very patchy mosaic of disturbed and relatively undisturbed forest (Figure 1, Foster and Boose 1992, Turner et al. 1997). For example, land surveyors in Maine described the effects of a massive windstorm in 1795, writing that "in many places the timber appeared almost all down—some places about half & some scarcely any" (Lorimer 1977:145). Such events, while creating new areas of young forest habitat, also leave islands or refugia of mature and old forest. These refugia can increase biological diversity and provide a source habitat for later colonization of disturbed areas by later successional species. Partial canopy removal also may provide suitable habitat for a mixture of species from different successional stages, as has been observed for songbird species following application of 2-aged management systems (Nichols 1996).

5) *Many severe disturbances do not initiate forest succession.* Disturbances such as intense crown fires and landslides result in "classical" forest succession because canopy and understory trees are usually destroyed and mineral soil is exposed, creating suitable seedbeds for pioneer species. Damage caused by wind, ice, drought, insects, and disease, on the other hand, is usually confined to the overstory, leaving the understory vegetation and forest floor largely intact. If a canopy of shade-tolerant species is destroyed by wind, insects, or logging, the new forest is usually recruited from the advance regeneration and no true succession occurs (Guldin and Lorimer 1985, Oliver and Larson 1996). This situation can be less favorable for certain early successional obligates such as ruffed grouse (*Bonasa umbellus*, Thompson and Dessecker 1997). Destruction of a canopy of early successional tree species such as aspen or pine, in fact, will usually accelerate forest succession by releasing the advance regeneration of shade-tolerant species (Foster 1988*a*, Abrams 1989). For this reason, a distinction is made in this paper between "early successional habitat" (meaning dominance by pioneer species such as aspen or pine) and "young forest habitat," which can include young stands of "late successional species" such as sugar maple (*Acer saccharum*).

Hemlock–northern hardwood–white pine region

Windstorms, ice storms, fire, drought, and insect and disease infestations are important agents of natural disturbance in the vast hemlock–northern hardwood–white pine region as mapped by Braun (1950), also called the Laurentian Mixed Forest Province (Region 211) by Bailey and Cushwa (1981). Late successional forests of shade-tolerant species blanketed the landscape over much of this region in presettlement times, but extensive stands of pines and other seral stages also occurred near the western border in Minnesota, parts of Ontario, and on drier habitats throughout the region. The most common large-scale destructive force in the hardwood-dominated sections is windstorms of various kinds, including thunderstorm downbursts, derechos (straight-line winds associated with thunderstorms), tornadoes, and hurricanes (in the southern half of New England). Blowdowns are recorded in virtually all of the presettlement land survey records, showing that the creation of large patches of young forest habitat must have been recurrent and common events across the entire region. More than 400 blowdowns were recorded in the nineteenth century land survey records of northern Wisconsin alone, with an average patch size of 94 ha (Canham and Loucks 1984). In the pine forests of Minnesota and Ontario, however, extensive fires were the dominant feature of the presettlement disturbance regime (Heinselman 1973; Cwynar 1977, 1978).

Other agents of natural disturbance such as ice storms, drought, insects, and disease also can cause substantial tree mortality, such as the 1998 ice storm that caused moderate to heavy damage over millions of hectares in the Northeast (Irland 1998). However, effects of these disturbances are more commonly diffuse, causing the death of scattered trees and patches rather than turnover of entire stands (e.g., Seischab et al. 1993, Parshall 1995).

Fire is the only natural disturbance agent normally capable of converting northern hardwood forests to aspen, paper birch, white pine, oaks, and other early or mid- successional species. However, intense fire is not common in mature maple–beech–hemlock stands on loam soils, in part because the finely compacted duff layer does not dry out readily and does not carry fire well. Although the ecological role of fire in northern hardwoods is not well understood, rate of fire spread and intensity are often sluggish even during severe droughts (Hawley and Hawes 1912, Miller 1978, Bormann and Likens 1979, Frelich and Lorimer 1991), giving northern hardwoods a reputation as the "asbestos forest" among fire control personnel. On upland sites with loamy soils, trees of all pioneer species combined typically made up only 5% or less of the presettlement forest and contemporary old-growth remnants (Mladenoff and Howell 1980, Whitney 1986, Lorimer and Frelich 1994). Sediment cores from northern hardwood watersheds usually contain low levels of charcoal and few indications of major fires in the several thousand years prior to European settlement (Patterson and Backman 1988, Clark and Royall 1996, Davis et al. 1998). Thus, fire frequency was apparently low even before decimation of Native American populations by European diseases.

In some situations, however, fire has played a more important role in landscapes with extensive northern hardwood forests. In the first few years after catastrophic blowdown, fine fuels remain very flammable. In northern Maine, the massive blowdown of 1795 caught fire about 8 years later, so that land surveyors in 1820 reported a tract of about 80,000 ha to be "universally blown down and burnt" (Lorimer 1977). In an 1860 description of one northern Wisconsin county, J. W. Hoyt noted that "there are also in these townships a great many windfalls, some of which are miles in length.... The fire runs through these windfalls every year or two, and kills all the vegetation...." (Curtis 1959:214). Crown fires or intense stand-killing surface fires also can occur in standing northern hardwood forests mixed with resinous conifers such as spruce (*Picea* spp.) and fir (*Abies* spp.). Risk increases on sites with gravelly, sandy, or shallow soils, and in places with numerous fallen or standing dead trees killed by insects or disease (Hawley and Hawes 1912, Darlington 1930).

Sandy outwash plains within the northern hardwood region, normally forested with pines, also supported a very different fire regime than the mesic forests of maple, hemlock, and beech (*Fagus grandifolia*) on loamy uplands. Surface fires burned frequently in the pine barrens (Curtis 1959) and crown fires had mean return times of about 60–170 years (Whitney 1986). Typical of early descriptions of the pine plains is that of geologist J. G. Norwood in 1847, who reported traveling across a sand plain in northern Wisconsin that supported only a "sparse growth of small pines and birch." Along the Wisconsin River, he noted that a "narrow strip of small pines line the banks of the river; but as you recede into the country, there are few trees of any size to be seen" (Curtis 1959: 173–174). Similar conditions prevailed on the sand plains of lower Michigan. In describing the vegetation of one township covered with sandy outwash, a land surveyor noted that "most of the township is...barrenly, being burnt over so often" (Whitney 1986:1556).

Some historic fires in the northern hardwood region were probably caused by Native American tribes, although the relative importance of anthropogenic fire has been debated (Day 1953, Patterson and Sassaman 1988). Setting fires to drive game, a common practice among tribes in other regions, was not often done in maple–beech–hemlock forests because "the beech and maple grounds were commonly too wet to be burned" (Dwight 1821, 4:38). However, in the mixed pine–oak forests of southern Ontario, missionary John Heckewelder wrote in 1798 that "we saw, and passed over, immense tracts of land, which had lately been set fire to by Indian hunters, and were in part still burning" (Wallace 1958:366). These observations are supported by lake sediment cores from southern Ontario, which show clear evidence of conversion from beech–maple forest to open country and oak–pine woods about A.D. 1400 (Delcourt 1987), and by fire-scar studies (Cwynar 1977, Guyette and Dey 1995). The high fire frequency documented on sandy outwash plains throughout the northern hardwood region probably was caused partly by Native Americans to encourage berry production and habitat for deer, because these drier habitats were burned more easily in most years (Dwight 1821, Whitney 1994, Loope and Anderton 1998).

Given the variety of disturbances in the northern hardwood region, how much open land and early successional habitat might have existed prior to European settlement? The northern hardwood region is one of the few regions in eastern North America for which reasonable quantitative estimates can be generated in response to this question. Although land survey records show that the landscape was peppered with sizable blowdowns and even large burned tracts in some places like northern Maine, cumulatively they occupied a fairly small proportion of the landscape in the northeastern quarter of the U.S. Estimates of blowdown coverage range from 0.2 to 3.5% of the land area in various parts of northern Wisconsin, Michigan, western New York, western Pennsylvania, and northern Maine (Table 1). To this must be added areas of recently burned lands and open pine barrens, which were common only in certain states. The total amount of forest less than 15 years old, including open barrens habitat, ranged from <1% to about 13% of the land area (Table 1).

Because of the low incidence of catastrophic disturbance, the vast maple–beech–hemlock stands on upland loamy soils probably were predominantly old-growth and uneven-aged, an inference supported by independent field studies (see review in Lorimer and Frelich 1994). These conditions presumably would have favored wildlife species that prefer late successional forests with multi-layered canopies and abundant coarse woody debris, such as pine marten (*Martes americana*), plethodontid salamanders, woodpeckers, and some mature-forest Neotropical migrant birds. It is well known that the chestnut-sided warbler (*Dendroica pensylvanica*), a common early successional species, was considered rare in the early nineteenth century and Audubon observed it only once (e.g., Forbush 1929). Yet why it was not commonly observed in recent blowdowns and barrens, many of which covered thousands of hectares, is not clear.

Table 1. Percentage of regional land area in young forest (one to 15 years old) and barrens habitat in presettlement times, based on early government land survey records in the northern hardwood region (Laurentian mixed forest province).

Location and dates	Recent blow-downs	Burned land & barrens	Total young forest	Citation
Northeastern Maine (1793–1827)	2.6	3.9	6.5	Lorimer 1977
Central New York (1790–1798)	0.2	0.1–0.6	0.3–0.8	Marks et al. 1992
West-central New York (1789–1792)	0.9	0.0	0.9	Seischab 1990
Western New York (1778–1798)	0.5	0.08 [a]	0.6	Seischab and Orwig 1991
Northern lower Michigan (1836–1859)	0.7	7.3	7.8	Whitney 1986
Eastern upper Michigan (1840–1856)	3.5	4.0	7.5	Zhang et al. 1999
Northern Wisconsin (1832–1865)	1.2	12.0 [b]	13.2	Curtis 1959, Canham & Loucks 1984

[a] Includes areas of standing dead trees for which cause was not specified

[b] The total proportion of northern Wisconsin listed by Curtis (1959) as "pine barrens" habitat, but not all of this area may have been young, scrubby vegetation.

Oak–hickory and oak–pine forests

Oak–hickory and oak–pine forests occupy numerous distinct physiographic provinces in eastern North America from the Ozark Highlands of Missouri to the coastal plain of the Southeast. Habitats range from somewhat poorly drained lowlands to dry, exposed ridgetops and mountain slopes. Therefore, disturbance regimes can vary widely depending on geographic location and site conditions.

Midwestern North America

Presettlement conditions are well known in the Midwest because there was little delay between Native American occupation and the land surveys and because the surveys themselves are systematic and relatively detailed. In contrast to the northern hardwood region, fire was a more pervasive force shaping the landscape in much of the central hardwood region. Most fire activity was apparently anthropogenic. Many early explorers, naturalists, and other travelers commented on frequent use of fire by Native Americans in the region. Natives burned woodlands to facilitate travel and hunting and to improve game habitat. This seems to be a majority opinion among ecologists and anthropologists today (although there have been some dissenters; see Raup 1937 and Russell 1983). Moore (1972) analyzed over 600 historical accounts of prairie fires in central North America and concluded that less than 0.5% were caused by lightning (cited in Whitney 1994:109). In the Great Lakes region, Loope and Anderton (1998) and Dey and Guyette (2000) reported that presettlement fire frequency was 10–40 times greater than lightning fire frequency in the twentieth century. Furthermore, Dey and Guyette (2000) found a strong spatial correlation between presettlement fire frequency and independent historical estimates of human population densities. In the southern

Appalachian region, historic fire statistics show that lightning fires are uncommon; most are ignited on high ridges and do not spread readily into lower elevations (Delcourt and Delcourt 1998).

Partly because of frequent anthropogenic fire, oak savannas and prairies were extensive in much of the Midwest, occupying approximately 46 million hectares of the "Prairie Peninsula" region in 8 states (Nuzzo 1986, Whitney 1994). Soil and topographic factors influenced the distribution of vegetation types within the region. Prairies in southern Wisconsin often occurred on very productive and well-drained soils, although they were more common on extensive level tracts of land where there were few barriers to fire spread. In Illinois, Indiana, and Ohio, however, many of the prairies were "wet prairies" located on poorly drained "depressional" sites alternatively subjected to very wet conditions in spring and very dry conditions in summer (Whitney and Steiger 1985, Whitney 1994). Throughout the Midwest, there was often an abrupt transition from oak savannas and prairies on the south and west sides of rivers to dense forests of fire-sensitive species on the north and east sides (e.g., Grimm 1984, Whitney and Steiger 1985, Leitner et al. 1991).

Estimates of the proportions of 8 midwestern states covered with prairie and oak savanna at the time of settlement have been recently summarized by Whitney (1994). For the present discussion I have excluded the northern portions of states like Wisconsin, Michigan, and Minnesota, which were covered largely by northern hardwoods and pine forest, to calculate the proportion of the central hardwood region covered by prairie and savanna habitat. This proportion ranged between 50 and 65% in southern Minnesota, southern Wisconsin, Illinois, and Missouri. Although reliable estimates are not currently available for Michigan, Whitney (1994:96) cites a knowledgeable surveyor who estimated that "somewhat more than half" of the lower peninsula consisted of "openings and plains." Indiana and Ohio had much less savanna and prairie habitat, with 20% and 4%, respectively.

Atlantic, Gulf slope, and Appalachian highlands

East of the Prairie Peninsula region, estimating the amount of grassland, savanna, and early successional forest habitat in presettlement times is difficult. The coastal plain and piedmont regions were settled very early and most of the areas lack detailed presettlement land surveys. Also, by the time "interior" territories like Kentucky and Tennessee were settled, nearly 150 years had elapsed since initial contact of native tribes with Europeans. During this time, native populations were decimated (possibly by 75–80% or more) by introduced diseases and warfare (Denevan 1992). Thus, forests encountered by European settlers in the early nineteenth century may have been less affected by fire than forests in previous centuries.

Despite these limitations, we can get some indication of the amount of early successional habitat from a variety of sources. Between 1500 and 1850, numerous credible observers described frequent woods burning by Native Americans and occurrence of extensive savanna or open woodland habitat across much of the eastern United States. For example, Verrazano saw "verie great fiers" when sailing along the Carolina coast in 1524, as did several 17th century mariners from Virginia to New Jersey (Day 1953). Johnson in 1654 wrote that the woods of coastal Massachusetts were "thin of timber in many places, like our Parkes in England." Lawrie in 1684 stated that in eastern New Jersey, "the trees grow generally not thick, but in some places ten, in some fifteen, in some twenty-five or thirty upon an acre" Whitney (1994:118).

Early travelers in the Southeast often described extensive savannas, even on upland sites in the piedmont. Near the Yadkin River in South Carolina, Lawson (1709: 51) wrote that "we travell'd this day, about 25 Miles, over pleasant Savanna Ground, high, and dry, having very few Trees upon it, and free from Grubs or Underwood." Near the Santee River, he described another savanna that was "over-flown with Water; where we were very short of Victuals, but finding the Woods newly burnt, and on fire in many Places, which gave us great Hope that Indians were not far off." John Smith's comment in 1630 that "all the woods for many an hundred mile" in Virginia "for the most part grow sleight" and have "much good ground betweene them without shrubs" (Arber 1910:950), might seem like a great exaggeration if it were not for similar descriptions in other reputable sources such as the journals of botanist William Bartram (Van Doren 1955).

The specific locations of some presettlement grasslands and savannas are well documented and sometimes even mapped. An extensive area of fire-created grassland on the Pennyroyal Plateau of Kentucky, approximately 250 km long and 20 km wide, is well documented from writings of the late eighteenth century (Baskin et al. 1994), as are grasslands and savannas in other parts of Kentucky, such as the Bluegrass region and the Jackson Purchase south of the Ohio River (Bryant and Martin 1988). Paleoecological evidence indicates that the Kentucky Barrens came into existence about 3,900 years ago, indicated by a dramatic rise in grass and prairie clover pollen in a nearby sink hole (Wilkins et al. 1991).

Examples of other specific mapped grassland sites include the Hempstead Plains of Long Island, the glades of southwestern Pennsylvania (Whitney 1994), prairies in and near the Black Belt of Alabama and Mississippi (Rostlund 1957), and possibly the Shenandoah Valley of Virginia (Kercheval 1833, but see contrary paleoecological interpretations in Craig 1969). In the early eighteenth century, there was sufficient grassland and savanna habitat in the Southeast and mid-Atlantic region to support significant herds of bison (*Bison bison*), for which there are numerous credible reports (Garretson 1938, Rostlund 1960). Settlers conducting a great "circle hunt" in 1760 near the Susquehanna River in Pennsylvania killed 111 bison, slightly more than the number of deer (Shelford 1963). Fire also is believed to have been important in maintaining canebakes (*Arundinaria* spp.). The apparent extinction of Bachman's warbler (*Vermivora bachmanii*) may have been caused partly by loss of cane habitat because of reduced fire frequencies (Engstrom 2000).

While the frequent occurrence of savannas, grasslands, and old fields near Native American settlements is well documented, it is unclear whether these open habitats were common across the entire landscape as they were in the Midwest. After the advent of agriculture about A.D. 1000, native villages typically became clustered along the floodplains of major rivers and streams, as indicated by archaeological evidence, historical evidence, and paleoecological evidence (e.g., Russell 1980, Mathis and Crow 1983, Delcourt 1987). It is uncertain if the "hinterlands" and remote upland areas were visited and burned frequently enough to maintain extensive savanna habitat. Early traveler descriptions may be somewhat misleading because people on these long journeys rarely strayed far from major navigable rivers and Indian trading paths. Areas in the Southeast described by the De Soto expedition as "thickly settled in numerous towns with fields extending from one to the other" (Rostlund 1957:395), were mainly on alluvial land "along the Savannah, Coosa, Alabama, and Tombigbee rivers and their tributaries" Sauer (1971:181). Delcourt (1987) concurred that, based on pollen and archaeological evidence, extensive cleared and open land in eastern Tennessee was probably confined to the major rivers. An example of how traveler descriptions might convey a misleading impression of landscapes dominated by open vegetation is illustrated by early accounts of the Ontario lowlands of western New York. Day (1953) relayed vivid and colorful descriptions from the seventeenth and early nineteenth centuries suggesting immense grassy fields and oak savannas in that region, but systematic land survey records show that beech–maple forest actually covered most of this landscape, at least at the end of the eighteenth century (Seischab 1990). Oak savannas and grasslands were apparently restricted to the vicinity of Iroquois village sites (Trigger 1969) and on drier, gravelly soils that were more easily burned (Dwight 1821, Maude 1826).

Although open grassland and savannas probably were restricted largely to the vicinity of native villages in coastal areas and near rivers, evidence suggests that fire was common enough on the more remote upland sites to alter forest density and species composition. Native hunters often traveled great distances from village sites on expeditions lasting several weeks and used fire to drive game (Loskiel 1794, Arber 1910). Perhaps most significant is the fact that land survey records reveal that enormous areas of the piedmont and Ridge and Valley provinces were heavily dominated on nearly all slope positions by fire-adapted species, such as various species of southern and northern pines (*Pinus taeda, P. virginiana, P. echinata, P. strobus*), post oak (*Quercus stellata*), white oak (*Q. alba*), and black oak (*Q. velutina*), with the addition of red oak (*Q. rubra*), chestnut oak (*Q. prinus*), and chestnut (*Castanea dentata*) in the higher elevations (Orwig and Abrams 1994; Abrams and Ruffner 1995; Cowell 1995, 1998; Abrams and MacCay 1996). These species are not very tolerant of shade and most have had difficulty in regenerating successfully on mesic and dry-mesic sites during the modern era of fire suppression (Abrams and Downs 1990, Abrams and Nowacki 1992, Lorimer 1993, Mikan et al. 1994).

Fire-scar evidence, paleoecological data, and historical descriptions of these upland habitats are limited, but available evidence is consistent with a hypothesis of frequent fire in the more remote upland oak–pine forests. Dey and Guyette (2000) reported multiple fire scars on seven oak–pine forest sites in south-central Ontario, with a mean fire interval of about 20 years for the period 1630–1850. Similar presettlement fire frequencies have been reported in Missouri, western Pennsylvania, the New Jersey piedmont, and western Maryland (Lutz 1930, Buell 1954, Abrams 2000, Guyette and Dey 2000). In Missouri, Guyette and Dey (2000) found evidence that population densities as low as 0.64 humans/ km^2 were sufficient for "pyro-saturation" of the landscape, with more than 30% of the landscape burning annually. Evidence of fires over the past several thousand years also has been reported from the pollen and charcoal record from sites in several physiographic provinces, including areas distant from floodplains of major rivers (Watts 1979, Patterson and Backman 1988, Maenza-Gmelch 1997, Delcourt and Delcourt 1998, Fuller et al. 1998). Neither the pollen record nor fire-scar studies suggest that presettlement fire frequency was markedly less than in the 150 years after settlement. Typical

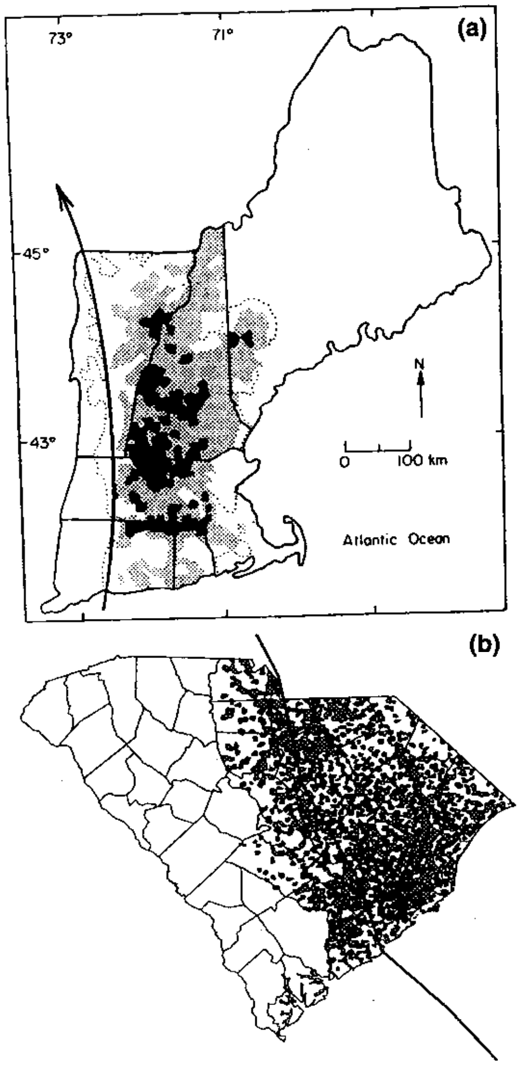


Figure 1. Atlantic hurricanes periodically cause extensive blowdown of forests in a wide swath across the landscape, even more than 100 km from the coast. Each map shown here depicts heavy damage on more than 500,000 ha, distributed in an intricate patchwork mosaic determined by topography, forest susceptibility, and pulses in hurricane intensity. (a) Pattern of damage caused by the 1938 hurricane in central New England. Light shading represents moderate damage and black indicates extensive damage (from Foster 1988a; reproduced with permission of the British Ecological Society). (b) Pattern of damage caused by Hurricane Hugo in South Carolina, 1989. Light shading represents light damage and black indicates moderate or heavy damage (from Sheffield and Thompson 1992, United States Forest Service). In both cases the arrow or dark line traces the central path of the hurricane.

post-settlement fire frequency in oak–hickory and oak–pine stands ranged from 7 to 30 years (Harmon 1982, Ross et al. 1982, Sutherland 1997, Sutherland et al. 1995, Abrams 2000, Dey and Guyette 2000).

There is unfortunately little direct evidence on structure of these upland oak-pine forests. But some historical evidence and experience with modern prescribed burns suggest several likely features. These forests probably often had heavy but not complete canopy closure and relatively little woody undergrowth. Featherstonhaugh (1844:50) reported that on the Cumberland Plateau of Tennessee, "the openness of the woods gives a parklike appearance to the country, and enables you to see through the forest for a great distance." Fralish et al. (1991) reported an estimated presettlement basal area of 15 m^2/ha across all slope positions in southern Illinois forests, which is only 65% of the basal area of current old-growth stands on comparable sites. The frequent fires probably did not greatly reduce tree longevity. Kalm (1772) noted that large trees in oak–hickory forests of eastern Pennsylvania most commonly reached ages of about 200 years and occasionally 300 years. Remnant stands surviving into the twentieth century were, in fact, often broadly uneven-aged (Ross et al. 1982, McGee 1984, Platt et al. 1988, Mikan et al. 1994, Abrams et al. 1997).

Although fire was probably the dominant disturbance force in oak and pine forests in many areas, other disturbances have been important to varying degrees. Hurricanes, for example, are extremely influential along the Atlantic slope. In recent times the 1938 hurricane in central New England (Foster 1988*b*) and the 1989 Hurricane Hugo in South Carolina (Sheffield and Thompson 1992) each destroyed more than 500,000 ha of forest in a patchy mosaic across the landscape (Figure 1). Central New England has been subjected to 3 destructive hurricanes since 1600, with a mean recurrence of only 150 years (Foster 1988*a*). In some cases these were followed by fire, leading to dominance by early successional species in even-aged stands. In the Southeast, Skeen et al. (1993) have suggested that extensive hurricane damage followed by fire may have been responsible for the origin of many southern pine stands in presettlement times.

Despite the tremendous wealth of evidence on the history and ecology of this region, the amount of early successional and savanna habitat in presettlement times seems to defy quantification without further and more explicit spatial evidence. After an exhaustive review of historical accounts from the sixteenth to the nineteenth centuries in the Southeast, Rostlund (1957:407) concluded, "how widespread [dense, closed-canopy forests] were in aboriginal time is hard to say, but it can be said that there are not many references in the early historic record to forests of this type.... [O]ne can hardly avoid drawing the conclusion that open woodland with little or no underbrush must have been the most common type of forest." Rostlund also concluded from historical evidence that these open forests were "mostly the work of man." In the subsequent 40 years, much new historic and scientific evidence has become available, but nearly all of this new evidence has simply reinforced Rostlund's conclusions on both counts. Had humans not crossed into North America 12,000 years ago, it seems likely that vegetation in these Atlantic provinces would have been quite different from that observed by the first Europeans. The occurrence of oak and pine forest probably would have been more restricted, perhaps mainly to dry ridges, upper slopes, other areas with dry sandy, gravelly, rocky, or thin soils, and burned windfalls. And regardless of the exact amount of open oak woodland and savanna habitat, most of it was probably anthropogenic and human-maintained. The main exception might be the extreme southern U.S., where lightning fires are much more frequent (Schroeder and Buck 1970).

Population dynamics of fauna in the rather open, fire-influenced oak–pine woodlands have not been investigated widely, so it is difficult to characterize the likely species composition and population levels of animals in the upland presettlement forests. Modern studies often have documented little change in bird, small mammal, and herpetofauna populations in response to prescribed burning of existing closed-canopy oak forests (Ford et al. 1999, Lyon et al. 2000). Some species, however, may be either positively or negatively affected, depending on the degree to which fire changes habitat features. For example, presettlement woodlands were probably more favorable for early successional birds such as indigo bunting (*Passerina cyanea*) and eastern bluebird (*Sialia sialis*) than the present oak forests, but less favorable for mature forest birds that nest on the ground or in low shrubs (see Aquilani et al. 2000, Lyon et al. 2000). Even more significant would be faunal differences between the open oak woodlands and the late successional maple and beech forests that would displace many oak stands in the absence of fire.

Post-settlement changes

From 1750 to 1880, forest cover in most of the eastern and midwestern states dropped to 10–30% of the landscape (Whitney 1994, Foster 1995). When clearing for agriculture was at its maximum, woodlot size in central Massachusetts followed a negative exponential distribution, with a mean of about 400 ha and a maximum size of 1,600 ha (Foster 1995). In contrast, mean size of woodlots in a township in southern Wisconsin was only 6–7 ha during the twentieth century (Whitney 1994).

A striking feature of the remaining forests at the height of agriculture was their young age in most areas. In 1885, more than 75% of the forest in central Massachusetts was less than 30 years old (Foster et al. 1998). By 1908, forests had increased to an average of 50% of the land area in 12 eastern states, but 56% of the forest was still classified as "cutover land" (Whitney 1994:192).

One reason for the young age of forests at that time was repeated coppicing of forest tracts to provide fuel for blast furnaces operated by iron companies and other industries. However, as Whitney (1994) has pointed out, 95% of all fuelwood consumption in the late nineteenth century was for domestic heating use. Thus, repeated cutting of woodlots for fuelwood, frequent fires on cutover land, and widespread farm abandonment were the major reasons for the young age of forests in the late nineteenth and early twentieth centuries.

Repeated clearcutting and fires in the late nineteenth and early twentieth centuries have had variable effects on species composition of contemporary stands. In some portions of the northern and central hardwood regions, forest species composition has not changed dramatically since presettlement times. However, beech, hemlock, and pine have declined in most northern forests, accompanied by an increase in aspen, paper birch, and maples. In Michigan, the aspen–paper birch type increased to 28% of the forest area by 1935, compared to <1% in presettlement times (Whitney 1994). Dramatic changes in fauna occurred in response to these habitat changes, not only because of decreased stand age, but also in response to compositional changes like the loss of conifers. For example, birds of mature conifer or mixed forests [e.g., Blackburnian warbler (*Dendroica fusca*,) and solitary vireo (*Vireo solitarius*)] declined sharply in the early twentieth century over extensive areas, whereas early successional species such as the chestnut-sided warbler and Philadelphia vireo (*Vireo philadelphicus*) showed corresponding increases (e.g., Kendeigh 1946, Whitney 1994).

With forest maturation in recent decades, these trends have reversed. Since 1935, area of aspen–birch has declined markedly, as much as 40% in Wisconsin (cf. Stone and Thorne 1961 vs. Schmidt 1997). In the central and southern region, oak and pine have maintained dominance, but bur oak (*Quercus macrocarpa*), post oak, and white oak have declined in most areas compared to presettlement conditions (Curtis 1959, Fralish et al. 1991).

Succession to more shade-tolerant species is well advanced in many oak–pine stands (e.g., McGee 1984, Hix and Lorimer 1991, Abrams and Nowacki 1992).

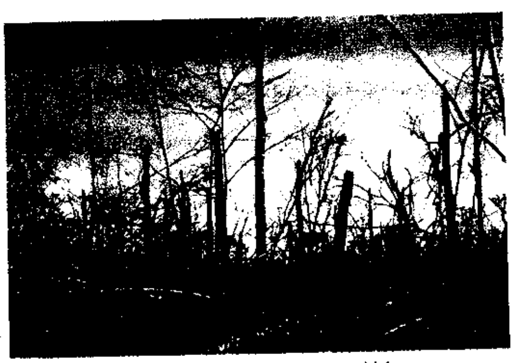
While the proportion of forest land has remained low in many midwestern states, abandonment of farmland in eastern states has resulted in a dramatic increase in the proportion of forest land since the turn of the twentieth century. Massachusetts is now 70% forested and parts of western New York and western Pennsylvania are 40–60% forested. Stand age also has increased, with the largest proportion in the 60- to 80-year class (Whitney 1994, Foster 1995). Young forest habitat now occupies 20% or less of total forest cover in many areas (e.g., Whitney 1990, Schmidt 1997, Foster et al. 1998, Trani et al. 2001). Thus, while stands in the northern versus central hardwood regions were quite different in structure and disturbance regime 300 years ago, imposition of modern anthropogenic disturbance regimes has caused them to pass almost simultaneously through similar stages of development, from the cutover, sapling-dominated phase of the early twentieth century to the currently dense, closed-canopy, even-aged stands that are now rapidly approaching maturity. Some of these stands probably resemble closely their counterparts on similar sites in presettlement times (Fralish et al. 1991). But on a larger scale, forests throughout the twentieth century have differed substantially in species dominance patterns, age structure, and density compared to those shaped by natural and anthropogenic disturbance between 1500 and 1850.

Conclusions and implications

Deciding on the optimal amount of early successional habitat on public lands is a complex ecological and social issue that can be guided only in part by scientific evidence. Information on historic, presettlement conditions can provide valuable input when formulating management policies for specific regions, or even landforms within a region. However, this review reinforces the common understanding among scientists that presettlement disturbance regimes were rather variable in time and space. Thus the question posed by Sprugel (1991: 1), "What is 'natural' vegetation in a changing environment?" is one that managers must consider whenever they use information on past conditions to establish management goals. One reason for using data on presettlement forests is that forest composition and dynamics are often relatively stable over moderate time spans of 500–2000 years. However, because of the possibility of global warming, it is not clear whether this generalization will apply in the near future.

Equally problematic is the evidence that many ecosystems in eastern North America were greatly shaped by a long history of anthropogenic fire. Some have proposed that Native American fires, in contrast to those set by European settlers, can be considered a natural part of the ecosystem (see the debate in Kilgore 1985). Given the extensive use of agriculture by some Native American tribes and large settlements at the time of first European contact, this distinction between native and settler fires may not be easy to justify for the late presettlement era. However, interpretation of Native American fires as "natural" may be more defensible for hunter–gatherer societies before the development of agriculture, on the grounds that these human populations were more constrained by natural ecosystems. In any event, widespread restoration of Native American fires in the central hardwoods region would involve reintroducing historical forces that had, in evolutionary terms, a relatively short-lived influence. As Kilgore (1985:61) notes, "We do not simulate other factors that have changed—extirpated plants and animals, Indian hunting, and Pleistocene glaciers. Why select Indian fire?"

For these reasons, there is room for different opinions on vegetation management, even among those who agree that ecosystem management provides the best paradigm for managing public lands. A goal to restore presettlement conditions and a goal to maintain or mimic natural disturbance processes may sound like similar or compatible philosophies. But the results of implementing these 2 different goals can in some cases be forests of radically divergent species composition, physiognomy, fauna, flora, and ecosystem dynamics. For example, a policy of using frequent prescribed burns to restore oak savannas



Severe disturbances often convert a mature or old forest to a young sapling stand without markedly changing tree species composition or initiating succession. The windstorm that destroyed the old-growth northern hardwood forest in this scene has simply released tall saplings of the same species, which will dominate the new forest canopy.

and open oak woodlands over extensive areas of the central hardwood region can be justified by citing fire as a natural process, and the fact that this vegetation was a dominant feature of the landscape in presettlement times. However, a case also could be made that the known natural disturbance regime (lightning fire, tornadoes, ice storms, etc.) appears incapable of maintaining extensive park-like oak stands or savannas, or even closed-canopy oak forest on many sites. In other words, on mesic and dry-mesic sites, oak forests often are not compositionally stable under the prevailing climate and natural disturbance regime. If natural forces were allowed to operate unimpeded, it is likely that forests of maple or other late successional species would eventually dominate rather large tracts in the central hardwood region. These might often be dense, old-growth forests shaped primarily by a small-gap disturbance regime (e.g., Runkle 1990, Abrams and Downs 1990). A decision between these 2 hypothetical management extremes (or an alternative in which managers use a variety of disturbance regimes) may be determined more by societal values and management budgets than by scientific arguments.

A more clearly defined role for scientific input might be questions on amount of habitat needed to maintain viable populations of early successional wildlife species, especially those currently or potentially at risk. This includes rare species (e.g., Kirtland's warbler, *Dendroica kirtlandii*) and relatively uncommon species with declining population trends, such as the golden-winged warbler (*Vermivora chrysoptera*, Smith et al. 1993). Resolution of this more restricted question is scientifically challenging because of the numbers of species involved and the large amount of data needed, especially on processes such as metapopulation dynamics that are still understood imperfectly. Other review papers in this special issue and future studies can perhaps contribute toward the resolution of this important question for specific groups of wildlife species.

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Conservation of disturbance-dependent birds in eastern North America

by William C. Hunter, David A. Buehler, Ronald A. Canterbury, John L. Confer, and Paul B. Hamel

Abstract Populations of most bird species associated with grassland, shrub-scrub habitats, and disturbed areas in forested habitats (hereafter all referred to as disturbance-dependent species) have declined steeply. However, a widespread perception exists that disturbance-dependent species are merely returning to population levels likely found by the first European explorers and settlers. The fact that many disturbance-dependent bird species and subspecies are now extinct, globally rare, threatened, or endangered challenges that perception and raises the question of balance between conservation efforts for birds dependent upon disturbances and birds more closely associated with mature forests. An overall understanding of the status and trends for these disturbance-dependent species requires reconstruction of at least thousands of years of Native American land use followed by 500 years of post-European settlement. Interpretations herein on how to manage for these disturbance-dependent species should support efforts to conserve all landbirds in eastern North America.

Key Words birds, disturbance, early succession, fire, grasslands, prairies, savanna, shrub-scrub

ost birds associated with open habitats have declined in eastern North America since at least the 1950s, with most eastern states recognizing some of these species on their state protected species lists (Vickery 1992, Askins 2000). These are species associated with a wide variety of natural open habitats including grasslands, prairies, savannas, glades and barrens, bogs, beaver meadows (floodplains), xeric scrublands, old-growth longleaf pine (*Pinus palustris*) forests, other pine communities, open (old-growth) oak woodlands, and (for some) tree-fall gaps in old-growth forests. Today, many of these species also are associated with active or abandoned farmland (i.e., old fields for the latter), restored coalfields, pastures, clear-cuts, utility rights-of-way, roadsides, and (for some)

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group-selection cuts in mature forests.

Species associated with open habitats are often classified as early successional, but many species also occur in mature or old-growth pine (*Pinus* spp.) and oak (*Quercus* spp.) forests where fire and grazing were principal disturbances during pre-European settlement times. Other species depend on trees in open settings such as savannas and open woodlands. Still other species require dense understories such as occur in sizable canopy gaps in mature forests. The common theme in habitat selection of all the above species is that their habitats are maintained by some form of disturbance. Thus, these species can be considered "disturbance-dependent," in contrast to forest-associated species that do not depend on disturbed habitats.

Disturbances in eastern forests take many forms, including fire, storms, grazing mammals (bison [*Bison bison*] and elk [*Cervus elaphus*]), beavers (*Castor canadensis*), forests managed commercially, and lands cleared (at least initially) for farming and development (Lorimer 2001).

Although an increasing number of species require heightened conservation attention, most effective conservation activity should be focused on entire communities.

Despite the declines underway, some species are still fairly common and widespread as deciphered from any standard bird field guide and from Breeding Bird Survey's relative abundance data (Sauer et al. 2000). Actually, declines during the last 50 years may have occurred after a 100- to 300-year expansion of suitable habitat following European settlement (Hamel and Buckner 1998; Askins 1999, 2000; Litvaitis et al. 1999). The clearing of the forests in eastern North America for European settlement allowed a diversity of successional habitats to coexist. However, the loss of these anthropogenic disturbances, along with decline of natural habitat conditions, now is resulting in significant declines for many species with a trajectory leading toward local extirpations for many species and extinctions for some others as discussed elsewhere (Litvaitis 1993, Litvaitis et al. 1999, Askins 2000).

We first review the species from eastern North America that are now extinct or nearly so, and vulnerable species and subspecies, from federally listed to those that may soon require listing without conservation action. We also describe the status of some representative disturbance-dependent species and review bird communities associated with grassland, shrub–scrub, savannas and open woodlands, and canopy gaps in mature forests. Finally, we discuss the role of "natural" and "anthropogenic" disturbances for conservation and suggest ways to integrate the needs of disturbance-dependent species with mature forest species through consideration of forest structure and landscape context.

Status review of disturbance-dependent or associated species

Species now extinct or nearly so

The extinction of the heath hen (*Tympanuchus cupido cupido*) was an early indication of the plight of disturbance-dependent species that was to come in eastern North America (Table 1). This subspecies of the greater prairie-chicken was common to locally abundant into the early 1800s. This gamebird's dependence on open habitats, particularly grassy oak woodlands and pine barrens, is well documented, but for all practical purposes these communities along the Atlantic seaboard were reduced, fragmented, and, with fire excluded, lost by 1800 (Askins 1999, Litvaitis et al. 1999). The last heath hen died on Martha's Vineyard, Massachusetts, in 1932 or 1933 (Bent 1932).

As with the heath hen, the first naturalists to encounter greater prairie-chickens (*T. c. pinnatus*) in the late 1700s and early 1800s in the Central Hardwoods and Eastern Tallgrass regions reported them as locally common in prairies and barrens (Palmer-Ball 1996). Today most of these populations are extirpated, with very small relict populations persisting elsewhere in the Midwest. A third subspecies, Attwater's prairie-chicken (*T. c. attwateri*), is federally endangered along the coastal prairies of Texas and is extirpated from the coastal prairies of Louisiana.

The extinct passenger pigeon (*Ectopistes migratorius*) and Carolina parakeet (*Conuropsis passerina*) fed on seeds and fruits that occurred most often in open, disturbance-maintained communities (Bent 1932, 1940), though the link between extinction and loss of disturbance-maintained habitats for these species is not as definitive as with the heath hen. The pigeon and parakeet are speculated to have used switchcane "canebrakes" (*Arundinaria gigantea*), a disturbance-maintained community formerly stretching in vast patches along many southern rivers, as roosting and feeding sites (Frost 1995, Platt and Brantley 1997). The Bachman's warbler (*Vermivora bachmanii*) may have foraged and nested primarily in large patches of canebrake, and the loss of this disturbance-maintained habitat may have contributed to this warbler's demise (Remsen 1986, Hamel 1995).

Only the plight of the ivory-billed woodpecker (*Camephilus principalis principalis*) in the southern United States surpasses the interest bird conservationists

Table 1. Extinct and federally listed endangered and threatened disturbance-dependent bird species in eastern North America. Unless otherwise cited, notes on disturbance-maintained communities used by these species are derived from Hamel (1992) and American Ornithologists Union (1998).

Taxon	Legal Status	Notes on use of disturbance-maintained communities used
Snail kite Everglades subsp. *(Rostrhamus sociabilis plumbeus)*	Endangered	Wet prairies and savannas, south-central FL.
Crested caracara Florida population *(Caracara cheriway audubonii)*	Threatened	Dry prairies and savannas, south-central FL.
Greater prairie-chicken Heath hen *(Tympanuchus cupido cupido)*	Extinct	Oak savannas, pine-oak barrens; New England–Mid Atlantic.
Greater prairie-chicken Attwater's subsp. *(T. c. attwateri)*	Endangered	Coastal prairies; central TX, extirpated LA.
Sandhill crane Mississippi subsp. *(Grus canadensis pulla)*	Endangered	Pine savannas; southern MS.
Whooping crane *(Grus americana)*	Endangered	Coastal prairies, marshes; south-central TX, extirpated LA, FL?
Eskimo curlew *(Numenius borealis)*	Endangered	Coastal prairies during northbound migration; LA and TX.
Passenger pigeon *(Ectopistes migratorius)*	Extinct	Old-growth forests, also fed on seeds and fruits in open country, possibly canebrakes (Platt and Brantley 1997).
Carolina parakeet *(Conuropsis carolinensis)*	Extinct	Old-growth forests, also fed on seeds and fruits in open, country, possibly canebrakes (Platt and Brantley 1997).
Red-cockaded woodpecker *(Picoides borealis)*	Endangered	Open, mature fire-maintained pine forests throughout South.
Ivory-billed woodpecker United States subspecies *(Campephilus principalis principalis)*	Endangered–extinct?	Old-growth forested wetlands; probably also old-growth fire-maintained southern pine forests throughout South (Jackson 1996).
Black-capped vireo *(Vireo atricapillus)*	Endangered	Dense, low fire-maintained thickets and oak shrub–scrub with many openings; central OK, TX.
Florida scrub-jay *(Aphelocoma coerulescens)*	Threatened	Fire-maintained xeric, low-growing oak scrub with scattered pines; peninsular FL.
Bachman's warbler *(Vermivora bachmanii)*	Endangered–extinct?	Not well known, but likely openings in old-growth forested wetlands, and especially canebrakes; MO and AK east to SC (Remsen 1986, Hamel 1995).
Kirtland's warbler *(Dendroica kirtlandii)*	Endangered	Shrub–scrub, jack pine after stand replacement burns; north-central MI(Botkin et al. 1991, Sykes 1997).
Grasshopper sparrow Florida subsp. *(Ammodramus savannarum floridanus)*	Endangered	Dry palmetto prairies and savannas; south-central FL.
Seaside sparrow Dusky subsp. *(Ammodramus maritimus nigrescens)*	Extinct	Wet prairies and savannas; upper St. Johns River, FL.
Cape Sable subsp. *(A. m. mirabilis)*	Endangered	Wet prairies and savannas; Everglades, south FL.

have for the Bachman's warbler. Ivory-billed woodpeckers require large expanses of old-growth forests for nesting and feeding. However, Jackson (1996) presents a strong case that this species' association with old-growth forests included fire-maintained southern pine communities (longleaf and slash [*P. elliottii* var. *densa*]) throughout Florida and bordering other major floodplains elsewhere. These forests were lost outside of Florida by the early 1800s, while in Florida such forests persisted into the early 1900s.

Federally listed

A second group of disturbance-dependent species are federally listed as endangered or threatened in all or part of their range (Table 1). Many federally listed species never responded to the flush of habitats created by settlement and today are very rare or still declining. A few federally listed species did experience some historical population stability or expansions, but landscape conditions are changing to the point that continued viability for these species is increasingly in question throughout their ranges.

A prime example of the latter group is the Kirtland's warbler's (*Dendroica kirtlandii*). Its total population size possibly increased during the initial settlement period when logging and slash fires provided a temporary but large increase in suitable nesting conditions (Askins 2000). This species is mostly restricted to the southern edge of the boreal-hardwood transitional forest in Michigan, but north of the regions formerly supporting prairies and savannas (Botkin et al. 1991). The Kirtland's warbler is dependent on jack pine (*Pinus banksiana*) and northern pin oak (*Quercus ellipsoidalis*) communities soon after stand-replacement burns on coarse Grayling sands (Sykes 1997). More recently, after many decades of fire suppression, a more modest population size was held stable for many years through a combination of local management and a program to reduce the brown-headed cowbird (*Molothrus ater*). Populations increased only due to larger landscape-level fires during the last decade. Unfortunately, the most appropriate management of Kirtland's warbler habitat is to use large, hot burns. Implementation of large-scale prescribed

Optimal breeding habitat for Henslow's sparrows at the southern end of their breeding range. Frequent disturbance through prescribed burning and live fire at Fort Campbell Military Reservation, Tennessee–Kentucky, provides and maintains these conditions. The predominant grass is little bluestem (*Andropogon scoparius*), and having scattered weedy patches to a few woody song perches appears to be important for this species as well. Photo by Michael Roedel, The Nature Conservancy.

burning is becoming more difficult as surrounding development and other land-use pressures come into conflict (Kepler et al. 1996). Present population increases now underway for Kirtland's warbler may not be sustained under conditions that are increasingly hostile to conducting effective landscape management.

National Watch List and other vulnerable birds

Many species associated with disturbance-maintained habitats may require elevated conservation attention in the near future. These are National Watch List species, species and subspecies identified by the United States Fish and Wildlife Service as being of conservation concern, or species in need of status review before future federal listing decisions may be made (Carter et al. 1996, 2000, Pashley et al. 2000, United States Fish and Wildlife Service Species of Conservation Concern, unpublished data). Among the highest-priority species and subspecies in need of conservation attention that make use of disturbance-maintained habitats are swallow-tailed kite (*Elanoides forficatus forficatus*), southeastern American kestrel (*Falco sparverius paulus*), Appalachian yellow-bellied sapsucker (*Sphyrapicus varius appalachiensis*), eastern and Appalachian Bewick's wrens (*Thryomanes bewickii bewickii, T. b. altus*), golden-winged warbler (*Vermivora chrysoptera*), cerulean warbler (*Dendroica cerulea*), Swainson's warbler (*Limnothlypis swainsonii*), Henslow's sparrow (*Ammodramus henslowii*), and eastern painted bunting (*Passerina ciris ciris*). Henslow's sparrow, golden-winged warbler, and cerulean warbler are the focus of much conservation interest today, with detailed status assessments either completed or nearly so (Pruitt 1996; Hamel 2000; Buehler et al., unpublished data).

Henslow's sparrow is perhaps the most vulnerable of the nonlisted nongame birds dependent on grasslands in eastern North America. This area-sensitive grassland species is rarely found in patches less than 30 ha (Smith 1992), with preferred patches >100 ha (Herkert et al.1993, Winter 1999, Winter and Faaborg 1999). Grassland habitats adjacent to hedgerows, treelines, or filter strips are avoided, perhaps because of elevated predator presence (O'Leary and Nyberg 2000, Winter et al. 2000). In addition, Henslow's sparrows prefer grasslands >30 cm tall with residual, standing vegetation from previous growing seasons, which in some areas include the first few years after a clearcut (Pruitt 1996).

Wintering populations of Henslow's sparrow occur primarily in open woodlands, particularly pine flatwoods and savannas, including pitcher plant (*Sarracenia* spp.) bogs. In addition, anthropogenically produced grassy habitats provide important wintering sites, especially in moist sites dominated by broomsedge (*Andropogon virginicus*) grasses (i.e., power rights-of-way, marsh edges, fallow fields). Henslow's sparrows may be most abundant on sites burned during the previous growing season, though birds occur on sites up to 2 years after dormant-season burns (Chandler and Woodrey 1995, Plentovich et al. 1999). However, when an area is being burned during winter, Henslow's sparrows and other wintering grassland birds are displaced from these sites, which may result in reduced overwinter survival (McNair 1998, Plentovich et al. 1998).

Golden-winged warbler is among the most vulnerable species dependent on early successional shrub–scrub habitats. Most golden-winged warbler territories now

Golden-winged warbler nesting location in alder swamp in upstate New York. The proportion of herbs, shrubs, and trees for this territory in a natural wetland looks very similar to the vegetation in many golden-winged warbler territories in human-generated sites undergoing succession. Photo by John Confer, Ithaca College, New York.

occur in secondary succession sites, such as abandoned farmland or clearcuts. In addition, this warbler uses alder bogs, tamarack swamps, and open woodlands with considerable understory. Within this wide range of habitat conditions, all territories provide patches of herbs with moderately dense growth and patches of shrubs or saplings, usually along a boundary with taller trees (Confer 1992, Howe et al. 1996). Historically, this warbler most likely was associated with abandoned beaver (*Castor canadensis*) meadows or other frequently disturbed habitats, including habitats subject to frequent burning (Brewster 1886; Short 1963; Confer unpublished data). Today, this species is associated with anthropogenic disturbances that mimic conditions that were more widespread prior to present-day suppression of fire and beavers. Golden-winged warbler "safe" areas today are concentrated in disturbance sites within boreal-hardwood transitional forests and at the higher elevations of the southern and central Appalachians.

Areas of golden-winged warbler abundance and high nesting success (Confer 1992, Klaus 1999) are generally either north of or at higher elevations than the present strongholds of the blue-winged warbler (*Vermivora pinus*). The golden-winged warbler has disappeared from most of the eastern portion of its range as the blue-winged warbler expanded eastward and northward, perhaps due to hybridization between the two species (Gill 1997). Prolonged coexistence of both species in the Hudson Highlands of southern New York is exceptional, and may be due to habitat segregation gained by golden-winged warblers that nest in locally abundant alder swamps (Confer et al. 1998).

Often golden-winged warbler territories include a forested edge along at least 25% of their territory and breeding birds are successful under a sparse canopied forest (Buehler et al., unpublished data). Potential territories in the middle of a large contiguous area (>40 ha) of abandoned farmland or clearcut lack this forest edge, and therefore few warblers occupy such "interiors" of shrub–scrub habitats (Confer 1992, unpublished data). Logging that leaves residual trees or uncut reserve areas within clearcuts could provide the needed forest edge in similarly large clearcut areas. Treatment areas of 12 to 20 ha, or leaving 10 to 20% residual canopy cover in larger treatment areas, and prescribed burning on a relatively long return interval (7 to 25 years, Frost 1995), could be used to maintain optimal habitat conditions over long periods of time for this species (Huffman 1997, Confer and Canterbury unpublished data).

At the other end of the successional spectrum are cerulean warblers, associated most often with mature hardwood-dominated forests (Robbins et al. 1992). Cerulean warblers are found to occupy the highest canopy layers for most of the breeding season, but habitat associations are complex and varied depending on landscape characteristics and disturbance histories (Hamel 2000). One feature that is emerging over much of the cerulean warbler's distribution is an affinity for openings adjacent to the largest trees in a stand, often creating a complex canopy structure. In addition to old-growth forests where tree-fall gaps may lead to suitable conditions, cerulean warblers also occupy mature forests adjacent to roadways (e.g., Blue Ridge Parkway in North Carolina and Virginia), areas recently subjected to shelterwood cuts or severe storm damage, and carefully managed private lands (Hamel et al. 1998, Hamel 2000).

Besides those species identified for conservation concern at the national level, other species also have declined precipitously in eastern North America. Some of these are still common and widespread elsewhere in North America and are therefore generally lower-priority species, including upland sandpiper (*Bartramia longicauda*), common ground-dove (*Columbina passerina*), loggerhead shrike (*Lanius ludovicianus*), and vesper sparrow (*Pooecetes gramineus*). These species still may be important in local conservation planning efforts, especially when higher-priority species are absent.

Disturbance-dependent bird communities

Although an increasing number of species require heightened conservation attention, most effective conservation activity should be focused on entire communities. Many disturbance-dependent species are not restricted to one habitat type, though many species are associated with grassy conditions, shrub–scrub conditions, savanna and open woodlands, or gaps in mature forests across community types. For eastern North America, we recognize 128 species that are associated with these conditions combined. About 60 other species of forest-associated landbirds are not obviously dependent upon disturbances in eastern North America. Although several of these species are frequently the subjects of forest bird conservation studies, none are considered vulnerable in eastern North America (e.g., barred owl [*Strix varia*], pileated woodpecker [*Dryocopus pileatus*], red-eyed vireo [*Vireo olivaceus*], pine warbler [*Dendroica pinus*], ovenbird [*Seiurus aurocapillus*], and scarlet tanager [*Piranga olivacea*]). In fact, only 2 nondisturbance-dependent forest species are on the Watch List (Bicknell's thrush [*Catharus bicknelli*] and prothonotary warbler [*Protonotaria citrea*]; Pashley et al. 2000). Fully 85% of these 60 species are not declining.

Table 2. Bird species in eastern North America associated with large areas with grass–herbaceous dominated ground conditions (includes prairies, savannas [pine and oak], bogs, glades, and barrens) early after disturbance.

Taxon	Watch list[a]	Continental trend[b]	Notes on disturbance-maintained habitat use[c]
Northern harrier (*Circus cyaneus*)		-* (BBS)	Grasslands, wet prairies with tallgrass, fields.
Rough-legged hawk (*Buteo lagopus*)		O (CBC)	Grasslands, open cultivated areas; winter.
Merlin (*Falco columbarius*)		O (CBC)	Open woodlands, grasslands, fields; winter.
Peregrine falcon (*Falco peregrinus*)		+ (BBS)	Open country usually near water; winter.
Greater prairie-chicken (*Tympanuchus cupido pinnatus*)	EH	- (BBS)	Tallgrass prairie with some agriculture nearby.
Northern bobwhite (*Colinus virginianus*)		-* (BBS)	Brushy fields, grasslands, fields, open woodlands.
Sandhill crane (*Grus canadensis*)		+* (BBS)	Wet pine savanna, wet prairies, adjacent grasslands and fields.
Killdeer (*Charadrius vociferus*)		-* (BBS)	Wide variety of open habitats, shortgrass, bare ground.
Upland sandpiper (*Bartramia longicauda*)		- (BBS)	Grasslands, especially prairies, dry meadows and pastures with tallgrass, airport margins.
Long-billed curlew (*Numenius americanus*)	M	-* (USSP)	Wet fields, wet grasslands; Coastal Prairies of TX and LA during winter.
Buff-breasted sandpiper (*Tryngites subruficollis*)	MH	- (USSP)	Dry grasslands with shortgrass, pastures, plowed fields; migration.
Common Snipe (*Gallinago gallinago*)		+ (BBS)	Wet meadows, wet fields, bogs.
Snowy owl (*Nyctea scandiaca*)		O (CBC)	Open country, prairies, fields, pastures, airports; winter.
Burrowing owl Florida subsp. (*Athene cunicularia floridana*)		- (BBS)	Dry Florida prairies, temporarily cleared lands.
Long-eared owl (*Asio otus*)		-* (CBC)	Roosts in forests, woodlots; forages in fields and meadows.
Short-eared owl (*Asio flammeus*)	M	-* (CBC)	Open country, prairies, meadows, savanna, with tall grass and moderate density of bare soil.
Common nighthawk (*Chordeiles minor*)		-* (BBS)	Wide variety of open habitat, especially savanna, grasslands, fields.
Horned lark (*Eremophila alpestris*)		-* (BBS)	Shortgrass, prairies, grazed pastures, open cultivated areas, bare soil.
Sedge wren (*Cistothorus platensis*)		+* (BBS)	Grasses, meadows, sedge meadows, wet fields with tallgrass and some bushes.
American pipit (*Anthus rubescens*)		-* (CBC)	Wet meadows, pastures, cultivated fields; winter.
Sprague's pipit (*Anthus spragueii*)	MH	-* (BBS)	Shortgrass, prairies, pastures and fields with medium grass; Coastal Prairies in LA and TX during winter.
Bachman's sparrow (*Aimophila aestivalis*)	EH	-* (BBS)	Open, grassy mature pine woods with scattered bushes, brushy–grassy hillsides, oldfields.
Vesper sparrow (*Pooecetes gramineus*)		-* (BBS)	Prairie, savanna, oldfields, woodland clearings.
Lark sparrow (*Chondestes grammacus*)		-* (BBS)	Open situations with scattered bushes and trees, prairie, savanna, cultivated areas.
Savannah sparrow (*Passerculus sandwichensis*)		-* (BBS)	Grasslands, meadows, bogs, farmlands, pastures.
Grasshopper sparrow (*Ammodramus savannarum*)		-* (BBS)	Prairie, old fields, open grasslands, pastures, savanna.
Henslow's sparrow (*Ammodramus henslowii*)	EH	-* (BBS)	Rank grass interspersed with weeds and shrubs, damp or low-lying areas, breeding; also pine savanna and flatwoods, bogs, with dense grass cover, winter.

(*continued*)

(See table notes next page)

Grassland and prairie communities

Grassland and prairie communities support species primarily associated with open treeless habitats. Over 99% of the original tall-grass prairie has been lost (Noss et al. 1995). Some prairie species now occur in man-made habitat in once-forested areas of the eastern United States. This only partially compensates for the decline of grassland species as prairies became wheat, corn, soybean, canola, and flax fields. However, some of these species may be found in habitats that may meet the definition of forests, such as sparsely stocked or open pine or oak communities subjected to frequent disturbances favoring grassy ground cover.

The plight of the 3 prairie-chicken subspecies in eastern North America, described above, is testimony to the loss of grasslands, prairies, savannas, and similar habitats. In fact, 8 of the 14 federally listed disturbance-dependent species and subspecies in eastern North America are associated with grassland, prairie, and savanna habitat (Table 1). About 70% of the 37 featured grassland-associated species are undergoing long-term declines or are recently declining in eastern North America (Table 2). Only 5 grassland-associated species appear to be increasing or are stable. For example, sedge wren (*Cistothorus platensis*) and Le Conte's sparrow

Table 2 (*continued*). Bird species in eastern North America associated with large areas with grass–herbaceous dominated ground conditions (includes prairies, savannas [pine and oak], bogs, glades, and barrens) early after disturbance.

Taxon	Watch list[a]	Continental trend[b]	Notes on disturbance-maintained habitat use[c]
Le Conte's sparrow (*Ammodramus leconteii*)		+ (BBS)	Moist grass, sedge meadows, tall rank grass, breeding; weedy fields, broomsedge; winter.
Lapland longspur (*Calcarius lapponicus*)		O (CBC)	Open grasslands, plowed fields, stubble; winter.
Smith's longspur (*Calcarius pictus*)	EH	O (CBC)	Fields with short grass, prairies, and grassy margins of airports; winter.
Snow bunting (*Plectrophenax nivalis*)		-* (CBC)	Grassy or weedy fields, stubble; winter.
Dickcissel (*Spiza americana*)	MH	-* (BBS)	Grasslands, meadows, savannas, cropland (alfalfa), and brushy fields.
Bobolink (*Dolichonyx oryzivorus*)	M	-* (BBS)	Tallgrass, flooded meadows, prairie, cultivated grains and alfalfa.
Red-winged blackbird (*Agelaius phoeniceus*)		-* (BBS)	Marshes, cultivated fields, breeding; plowed fields, prairies, pastures, cultivated lands, winter.
Eastern meadowlark (*Sturnella magna*)		-* (BBS)	Grassland, savanna, open fields, pastures, and cultivated lands.
Brewer's blackbird (*Euphagus cyanocephalus*)		-* (BBS)	Pastures and fields; winter.
Brown-headed cowbird (*Molothrus ater*)		-* (BBS)	Feeds primarily cultivated lands, fields, pastures.

[a] Watch List species are identified as in need for conservation attention at the national level (EH = extremely high priority, MH = moderately high priority, M = moderate priority; Carter et al. 1996, 2000).

[b] Continental population trends for this and subsequent tables are mostly from Breeding Bird Survey (BBS, 1966–1999; http://www.mbr.nbs.gov/bbs/bbs.html; Sauer et al. 2000), Christmas Bird Count (CBC, 1959–1988; Butcher 1990), or United States Shorebird Plan (USSP; http://www.Manomet.org/USSCP.htm). Population trends are interpreted following Table 4 in Carter et al. (2000) as follows: -* = significant decrease, - = possible decrease, O = trend uncertain, + = stable or possible increase, +* = significant increase.

[c] Habitat descriptions as they relate to disturbance-maintained conditions are adapted mostly from AOU (1998) or Hamel (1992). Species breed unless otherwise indicated as primarily migrating or wintering in eastern North America.

(*Ammodramus leconteii*) may benefit during the breeding season from habitat expanding under United States Department of Agriculture Natural Resources Conservation Service's Conservation Reserve Program in the eastern Great Plains (Johnson and Igl 1995, Igl and Johnson 1999, Peterjohn and Sauer 1999). Similarly, these same species make great use during winter of the early stages of afforestation now underway in much of the Southeast through programs such as United States Department of Agriculture's Wetland Reserve Program and similar private land-restoration initiatives (P. Hamel, personal observation).

Grassland patch size appears to be an important factor limiting distribution of many grassland species. Greater prairie-chickens and Henslow's sparrows especially appear to be area-sensitive and occur only in the largest habitat patches. In addition, other species (e.g., dickcissel [*Spiza americana*]) appear to be demographically area-sensitive by consistently occupying small habitat patches but suffering high and generally unsustainable rates of nest depredation and cowbird parasitism (Winter 1999, Winter and Faaborg 1999). Still other grassland species (e.g., Bachman's sparrow [*Aimophila aestivalis*]) may not easily disperse from one suitable habitat patch to another newly developing patch separated by unsuitable habitats without connecting grassy-dominated corridors (Dunning et al. 1995).

Shrub–scrub communities

Shrub–scrub communities include habitat patches with woody plants that are typically <3 m tall. Natural shrub–scrub communities include Florida's Lake Wales Ridge and coastal scrublands, bog and swamp–shrub communities, and barrens and glades where fire or other disturbances are regular, but with a longer duration between major fire events than would support more grass-dominated communities. Some shrub–scrub species, notably the golden-winged warbler, occur in dry uplands and wetlands. Both conditions are becoming rare; for example, in pre-colonial New York, beaver-caused floodplains occurred on about 1 million acres (3.5% of New York), although this disturbance habitat is now reduced by 65% (Gotie and Jenks 1982). Species associated with shrub–scrub communities also make great use of old fields, abandoned farmland, restored coalfields, utility rights-of-way, and regenerating clearcuts in the shrub–scrub or seedling–sapling stage of succession.

Three federally listed shrub–scrub-associated species in eastern North America are the Kirtland's warbler in Michigan, black-capped vireo (*Vireo atricapillus*) in Texas and Oklahoma, and Florida scrub-jay (*Aphelocoma coerulescens*) restricted to peninsular Florida (Table 1). About 70% of the 40 featured nonlisted shrub–scrub species are undergoing long-term declines or are recently declining in eastern North America (Table 3). Only 10

Table 3. Bird species in eastern North America associated primarily with large patches (e.g., greater than 5 ha) with shrub–scrub, early successional, and forest edge conditions generally more than 3 years after disturbance.

Taxon	Watch list[a]	Continental trend[b]	Notes on disturbance-maintained habitat use.[c]
Ruffed grouse (*Bonasa umbellus*)		O (CBC)	Mixed and deciduous woodlands with openings, oak savannas.
Wild turkey (*Meleagris gallopavo*)		+* (BBS)	Open woodlands, especially with adjacent or clearings pastures.
American woodcock (*Scolopax minor*)	MH	-* (USSP)	Moist woodlands, thickets along streams or in boggy areas, usually near wet grassy meadows and fields.
Mourning dove (*Zenaida macroura*)		-* (BBS)	Savannas, cultivated lands with scattered trees, brushy areas, open woodlands.
Common ground-dove (*Columbina passerina*)		-* (BBS)	Arid lowland scrub, second-growth scrub, pastures, cultivated lands.
Black-billed cuckoo (*Coccyzus erythropthalmus*)		-* (BBS)	Woodland edges, deciduous thickets, shrubby places, and brushy edges of second-growth.
Smooth-billed ani (*Crotophaga ani*)		-* (Other)	Second-growth scrub; south FL.
Whip-poor-will (*Caprimulgus vociferus*)		-* (BBS)	Forest and open woodlands, forages over open areas.
Alder flycatcher–Willow flycatcher (*Empidonax alnorum–E. traillii*)		O (BBS)	Moist, brushy thickets, open second growth, alder swamps.
Least flycatcher (*Empidonax minimus*)		-* (BBS)	Open deciduous woodlands, forest edge.
Bell's vireo (*Vireo bellii*)	EH	-* (BBS)	Dense brush, willow thickets, streamside thickets, scrub oak.
Warbling vireo (*Vireo gilvus*)		+* (BBS)	Open woodlands often near water.
Philadelphia vireo (*Vireo philadelphicus*)		+* (BBS)	Open woodland, forest edge, second growth, and alder and willow thickets.
Bewick's wren Eastern subsp., Appalachian subsp. (*Thryomanes bewickii bewickii, T. b. altus*)		-* (BBS)	Brushy areas, thickets, scrub in open country, brushy edges of woodlands, brush piles.
Veery (*Catharus fuscescens*)		-* (BBS)	High elevation hardwood and swamp forest, especially areas with shrubby understory, second growth.
Blue-winged warbler (*Vermivora pinus*)	M	+ (BBS)	Second-growth dominated by shrubs, from old fields to forest edge.
Golden-winged warbler (*Vermivora chrysoptera*)	EH	-* (BBS)	Tamarack bogs, alder swamps, second-growth, old fields, dominated by shrubs, saplings, and herbaceous growth.
Orange-crowned warbler (*Vermivora celata*)		O (CBC)	Variety of wooded habitat edges, especially with dense undergrowth.
Nashville warbler (*Vermivora ruficapilla*)		+* (BBS)	Open, brushy woodland, second growth, regenerating burns and clearcuts, bogs, brushy riparian.
Yellow warbler (*Dendroica petechia*)		+ (BBS)	Riparian woodlands, particularly willow, early succession dominated by saplings, regenerating burns and clearcuts.
Chestnut-sided warbler (*Dendroica pensylvanica*)		-* (BBS)	Early successional woodlands, mountain laurel thickets, forest edge.
Prairie warbler (*Dendroica discolor*)	M	-* (BBS)	Brushy second growth, dry scrub ridgetops, barrens, mature southern pine, regenerating burns and clearcuts.
Palm warbler (*Dendroica palmarum*)		-* (CBC)	Open boreal areas with heavy undergrowth and scattered trees, breeding; second-growth, fields, and edges, winter.
Northern waterthrush (*Seiurus noveboracensis*)		+ (BBS)	Thickets near slow streams, ponds, swamps, bogs.
Connecticut warbler (*Oporornis agilis*)		-* (BBS)	Spruce and tamarack bogs, locally jack pine barrens.
Mourning warbler (*Oporornis philadelphia*)		-* (BBS)	Open brushy woodland and second growth, especially regenerating burns and clearcuts.
Common yellowthroat (*Geothlypis trichas*)		-* (BBS)	Thickets near water, bogs, brushy pastures, oldfields, regenerating clearcuts.
Wilson's warbler (*Wilsonia citrina*)		-* (BBS)	Riparian thickets of alder and willow, moist undergrowth, dense second-growth and bogs.

(*continued*)

(See table notes next page)

species are increasing or are stable in eastern North America. One of the increasing species is wild turkey (*Meleagris gallopavo*), benefiting from several decades of intensive and widespread management attention. Among the 6 nongame species undergoing increases, 3 are associated with either burning or logging activities ongoing in boreal hardwood transitional forests and may be disproportionately benefiting from such activity, particularly Nashville warbler (*Vermivora ruficapilla*), compared with co-occurring species undergoing declines (Schulte and Niemi 1998). In the Southeast, only one nongame species is definitely increasing, the blue grosbeak (*Guiraca caerulea*).

Despite some hopeful population trends for a few shrub–scrub species, most are declining steeply. Some of these species also exhibit area-sensitivity. For example, golden-winged warblers mostly avoid small patches (<2 ha) and begin to increase in occupancy and densities at patch sizes >12 ha up to 40 ha (Buehler et al., unpublished data). In addition to golden-winged warbler, other shrub–scrub species may exhibit some form of area-sensitivity, but more work is needed to clarify how large patch sizes need to be—first to predict species presence and second for such species to exhibit high levels of reproductive

Table 3 (*continued*). Bird species in eastern North America associated primarily with large patches (e.g., greater than 5 ha) with shrub–scrub, early successional, and forest edge conditions generally more than 3 years after disturbance.

Taxon	Watch list[a]	Continental trend[b]	Notes on disturbance-maintained habitat use.[c]
Yellow-breasted chat (*Icteria virens*)		-* (BBS)	Dense second-growth, riparian thickets, brush, and regenerating clearcuts.
Rufous-crowned sparrow (*Aimophila ruficeps*)		- (BBS)	Brush, scattered scrub or short trees, grassy patches, Ouachitas of Arkansas and Oklahoma.
American tree sparrow (*Spizella arborea*)		-* (CBC)	Weedy fields, brush, and hedgerows; winter.
Clay-colored sparrow (*Spizella pallida*)		-* (BBS)	Brushy fields, groves, streamside thickets.
Field sparrow (Spizella pusilia)		-* (BBS)	Old fields, brushy hillsides, overgrown pastures, sparse second growth, hedgerows.
Lincoln's sparrow (*Melospiza lincolnii*)		+* (BBS)	Bogs, wet meadows, riparian thickets, dry brushy clearings.
Swamp sparrow (*Melospiza georgiana*)		+* (BBS)	Bogs and wet meadows, breeding; weedy fields, brush, thickets, forest edge, shrub-scrub wetlands, winter.
Harris' sparrow (*Zonotrichia querula*)	MH	-* (CBC)	Thickets, open woodlands, forest edge, windbreaks, hedgerows, scrub; winter.
White-crowned sparrow (*Zonotrichia leucophrys*)		-* (CBC)	Thickets, farmlands; winter.
Blue grosbeak (*Guiraca caerulea*)		+* (BBS)	Brushy and weedy fields, young second growth, riparian thickets.
Painted bunting (*Passerina ciris*)	MH	-* (BBS)	Partly open situations with dense brush and scattered trees, riparian thickets, weedy and shrubby areas.
Orchard oriole (*Icterus spurius*)		-* (BBS)	Scrub, second growth, brushy hillsides, with scattered trees, open woodlands, orchards.

[a] Watch List species are identified as in need for conservation attention at the national level (EH = extremely high priority, MH = moderately high priority, M = moderate priority; Carter et al. 1996, 2000).

[b] Continental population trends for this and subsequent tables are mostly from Breeding Bird Survey (BBS, 1966–1999; http://www.mbr.nbs.gov/bbs/bbs.html; Sauer et al. 2000), Christmas Bird Count (CBC, 1959–1988; Butcher 1990), or United States Shorebird Plan (USSP; http://www.Manomet.org/USSCP.htm). Population trends are interpreted following Table 4 in Carter et al. (2000) as follows: -* = significant decrease, - = possible decrease, O = trend uncertain, + = stable or possible increase, +* = significant increase.

[c] Habitat descriptions as they relate to disturbance-maintained conditions are adapted mostly from AOU (1998) or Hamel (1992). Species breed unless otherwise indicated as primarily migrating or wintering in eastern North America.

success (Rudnicky and Hunter 1993, Burhans and Thompson 1999).

Open woodlands and savanna communities for species requiring trees

Open woodlands are those communities that support mature trees but in densities at which substantial light reaches the ground and disturbances support mostly grass-dominated ground cover. At longer return intervals, some patches of shrub–scrub cover also may be retained in patches of regenerating pine or hardwood. Midwestern savannas (particularly oak-dominated) are stocked sparsely with trees and represent transitional habitats from woodlands to prairies through much of eastern North America. Noss et al. (1995) consider these habitat conditions as critically endangered ones. Species included here are those that require trees but are otherwise associated with open habitats. Many species treated in grassy and shrub–scrub-dominated habitats also may occur in open woodlands and savannas, but do not require trees.

Red-cockaded woodpecker (*Picoides borealis*) is the best-known federally listed species dependent upon open pine forests (Kulhavy et al. 1995). The red-cockaded woodpecker is a very strict specialist in terms of its cavity requirements, almost always in live pines with red-heart disease. However, many other species require open woodland conditions in eastern North America. Some of these species co-occur with red-cockaded woodpecker, but may require management attention over and above that given to this endangered species (e.g., southeastern American kestrel; Saenz et al. 1998).

About 70% of 21 featured species associated with open woodlands and savannas are undergoing long-term declines or are declining recently in eastern North America (Table 4). Only 2 species show increasing or stable population trends, with the eastern bluebird (*Sialia sialis*) obviously benefiting from popular nest-box programs throughout eastern North America. The other species possibly increasing is the swallow-tailed kite, but it still numbers only about 5,000 total individuals and remains one of the highest-priority species in need of conservation action in eastern North America (Meyer 1995).

Among widespread and relatively common species associated with savanna or open woodlands are red-headed woodpeckers (*Melanerpes erythrocephalus*), loggerhead shrikes, and brown-headed nuthatches (*Sitta pusilla*), all of which have declined greatly. Despite supposedly ample habitat conditions in rural landscapes (orchards, pine plantations, farmlands with hedgerows, and trees forming shelterbelts), these conditions are inadequate to support many of these species, as evidenced by

Table 4. Bird species associated with disturbance-maintained woodlands, principally native pine and open oak woodland and savanna communities.

Taxon	Watch list[a]	Continental trend[b]	Notes on disturbance-maintained habitat use[c]
Swallow-tailed kite (*Elanoides forficatus forficatus*)	EH	+ (BBS)	Open pine savannas, feeds over fields, edges adjacent to largely forested areas.
White-tailed kite (*Elanus leucurus*)		O (BBS)	Savanna, open woodland, cultivated fields; FL.
Mississippi kite (*Ictinia mississippiensis*)		O (BBS)	Open woodlands, prairies near riparian woodlands.
American kestrel (*Falco sparverius paulus*)		-* (BBS)	Open country with scattered trees, longleaf and other open mature pine forests in South; cavity nester.
Yellow-billed cuckoo (*Coccyzus americanus*)		-* (BBS)	Open woodland, especially with thick undergrowth , orchards, and streamside groves.
Barn owl (*Tyto alba*)		- (BBS)	Open country, grasslands, cultivated lands; cavity nester.
Chuck-will's-widow (*Caprimulgus carolinensis*)	M	-* (BBS)	Open pine and oak woodlands, feeds within open forests.
Red-headed woodpecker (*Melanerpes erythrocephalus*)	M	-* (BBS)	Open woodlands, pine and oak, savannas; cavity nester.
Yellow-bellied sapsucker (*Sphyrapicus varius*)		+ (BBS)	Deciduous and mixed forests, forest edges near bogs and meadows, regenerating hardwoods; cavity nester.
Northern flicker (*Colaptes auratus*)		-* (BBS)	Open woodlands, savannas with scattered trees and snags; cavity nester.
Olive-sided flycatcher (*Contopus cooperi*)		-* (BBS)	Subalpine conifer forests, spruce bogs, burned areas with standing dead trees.
Eastern wood-pewee (*Contopus virens*)		-* (BBS)	Open woodlands, forest edges.
Eastern kingbird (*Tyrannus tyrannus*)		-* (BBS)	Open country with scattered trees and shrubs.
Scissor-tailed flycatcher (*Tyrannus forficatus*)		-* (BBS)	Open country, especially dry grasslands, savanna, scrub, cultivated lands with scattered shrubs and trees.
Loggerhead shrike (*Lanius ludovicianus*)		-* (BBS)	Open country with scattered trees and shrubs, cultivated land, pastures, savanna.
Brown-headed nuthatch (*Sitta pusilla*)	MH	-* (BBS)	Open mature pine and pine-oak woodlands; cavity nester.
Eastern bluebird (*Sialia sialis*)		+* (BBS)	Open woodlands, cultivated areas with scattered trees; cavity nester.
Summer tanager (*Piranga rubra*)		- (BBS)	Open woodlands, including mature southern pine and oak savannas.
Baltimore oriole (*Icterus galbula*)		-* (BBS)	Open woodlands, forest edge, riparian woodland, orchards.
Common redpoll (*Carduelis flammea*)		O (CBC)	Open woodlands, weedy fields, fencerows; winter.
American goldfinch (*Carduelis tristis*)		- (BBS)	Open woodlands, forest edge, second growth, orchards, weedy fields, cultivated lands.

[a] Watch List species are identified as in need for conservation attention at the national level (EH = extremely high priority, MH = moderately high priority, M = moderate priority; Carter et al. 1996, 2000).

[b] Continental population trends for this and subsequent tables are mostly from Breeding Bird Survey (BBS, 1966–1999; http://www.mbr.nbs.gov/bbs/bbs.html; Sauer et al. 2000), Christmas Bird Count (CBC, 1959–1988; Butcher 1990), or United States Shorebird Plan (USSP; http://www.Manomet.org/USSCP.htm). Population trends are interpreted following Table 4 in Carter et al. (2000) as follows: -* = significant decrease, - = possible decrease, O = trend uncertain, + = stable or possible increase, +* = significant increase.

[c] Habitat descriptions as they relate to disturbance-maintained conditions are adapted mostly from AOU (1998) or Hamel (1992). Species breed unless otherwise indicated as primarily migrating or wintering in eastern North America .

continued declines (e.g., Pruitt 2000).

Forest openings in hardwood or mixed forest communities

Forest openings are habitats developing after disturbances that may occur from tree-fall gaps in old-growth forests or from other disturbances, natural and anthropogenic. We include species here that inhabit these openings or the edges around openings, but are otherwise characterized as forest-associated species.

No federally listed species depends on forest openings as defined here. Over 45% of the 30 species featured are undergoing long-term declines or are recently declining in eastern North America (Table 5). Twelve species have stable or increasing trends, 5 of which may be benefiting from ongoing timber harvests in boreal-hardwood transitional forests. However, other co-occurring species are undergoing declines in these same forests, such as bay-breasted warbler (*Dendroica castanea*), Canada warbler (*Wilsonia canadensis*), and white-throated sparrow (*Zonotrichia albicollis*).

The proportion of declining species within this group of featured species is low compared with other groups. This highlights a possible difference in the relative threat between species associated with smaller disturbances in mature forests and the previous 3 groups of species dependent on larger-scale and more frequent disturbances. Still, the number of declining species associated with openings in mature forests is double that for increasing species. The declines documented for species dependent on openings (less than 4 ha) within mature forests does suggest that some managed disturbance may be warranted, or compatible at least, to support mature forest-associated species (Kilgo et al. 1996, Morse and Robinson 1998).

Table 5. Bird species associated with disturbances within forests, especially small (<4 ha) but also for some species larger patches.

Taxon	Watch list[a]	Continental trend[b]	Notes on disturbance-maintained habitat use[c]
Spruce grouse (*Falcipennis canadensis*)		+* (CBC)	Spruce and other conifer forests, with dense cover of grasses and shrubs as in burned areas.
Three-toed woodpecker (*Picoides tridactylus*)		O (BBS)	Spruce and other conifers, favoring areas with many large dead trees, such as burns and insect outbreaks.
Black-backed woodpecker (*Picoides arcticus*)		O (BBS)	Spruce and fir forests, especially windfalls and burned areas with standing dead trees.
White-eyed vireo (*Vireo griseus*)		+ (BBS)	Dense undergrowth at deciduous forest edge and treefalls.
Blue-gray gnatcatcher (*Polioptila caerulea*)		+* (BBS)	Deciduous forests, pine-oak woodlands breeding; in winter dense second-growth, dense.
Swainson's thrush (*Catharus ustulatus*)		- (BBS)	Dense scrub, coniferous (spruce) woodland with dense undergrowth, second growth, thickets.
Hermit thrush (*Catharus guttatus*)		+* (BBS)	Open coniferous and mixed forest, sparse jack-pine.
Wood thrush (*Hylocichla mustelina*)	MH	-* (BBS)	Deciduous forest and woodland, locally dense second-growth with dense shrub layer.
Gray catbird (*Dumetella carolinensis*)		+ (BBS)	Thickets, dense brushy areas, undergrowth along forest edge.
Brown thrasher (*Toxostoma rufum*)		-* (BBS)	Thickets and brushy areas in forest clearings and forest edge, shrubby areas.
Tennessee warbler (*Vermivora peregrina*)		O (BBS)	Open woodlands with brushy undergrowth and herbaceous ground cover.
Magnolia warbler (*Dendroica magnolia*)		+* (BBS)	Open moist spruce-fir or mixed forest, forest edge, second-growth.
Cape May warbler (*Dendroica tigrina*)		O (BBS)	Spruce forest usually open, spruce bogs.
Black-throated blue warbler (*Dendroica caerulescens*)	MH	+ (BBS)	Deciduous or mixed woodland and second growth with dense understory.
Bay-breasted warbler (*Dendroica castanea*)	M	- (BBS)	Boreal forest with openings, occasionally second growth and deciduous scrub.
Cerulean warbler (*Dendroica cerulea*)	EH	-* (BBS)	Mature deciduous forests, usually tall trees present, complex canopies often near canopy gaps.
Black-and-white warbler (*Mniotilta varia*)		+ (BBS)	Mature forests, tall trees present, dense understory.
American redstart (*Setophaga ruticilla*)		- (BBS)	Open woodlands, riparian (cottonwood and willow), and second growth.
Worm-eating warbler (*Helmitheros vermivorus*)	MH	+ (BBS)	Deciduous forest and damp, brushy ravines with dense undergrowth, regenerating clearcuts.
Swainson's warbler (*Limnothlypis swainsonii*)	EH	+* (BBS)	Forested wetlands with dense undergrowth and sparse ground cover; dense second growth and canebrakes; also rhododendron thickets in mountains.
Kentucky warbler (*Oporornis formosus*)	M	-* (BBS)	Deciduous forest with dense herbaceous undergrowth, dense second growth, shady ravines,swamp edges.
Hooded warbler (*Wilsonia citrina*)		+ (BBS)	Deciduous and mixed forest with dense understory near streams, ravines, second growth.
Canada warbler (*Wilsonia canadensis*)		-* (BBS)	Moist woodland with dense undergrowth, bogs and tall scrub along streams.
Eastern towhee (*Pipilo erythrophthalmus*)		-* (BBS)	Dense second growth, undergrowth of open woodland, forest edge.
Fox sparrow (*Passerella iliaca*)		+ (BBS)	Undergrowth of forests, forest edge, woodland thickets, breeding; variety of habitats with thickets.
White-throated sparrow (*Zonotrichia albicollis*)		-* (BBS)	Forests, forest edge with dense understory, clearings and bogs.
Dark-eyed junco (*Junco hyemalis*)		-* (BBS)	Forests, forest edge, clearings, bogs, brushy areas, open woodlands.
Rose-breasted grosbeak (*Pheucticus ludovicianus*)		-* (BBS)	Open forest, forest edge, woodland, tall second growth.

(continued)

(See table notes next page)

Managing mature forest and disturbance-dependent species in the same landscapes

Many disturbance-maintained ecosystems have been lost from the eastern North American landscape during the last 300 years. The only evidence of their former extent is etched in the memoirs of the first European explorers, naturalists, and settlers. Robbins (1996) describes the pre-settlement Maryland landscape as likely rich in diversity of relatively stable early successional habitats in large patches, otherwise embedded within mature and old-growth forests. While there is a common misconception that many disturbance-dependent species moved into the East from the West, or into the Northeast from the Southeast, Robbins (1996: 20) suggests otherwise:

> "It is more likely, however, that most of these purported immigrants were native to the natural openings in the presettlement landscape. The upland sandpiper, northern harrier [*Circus cyaneus*], loggerhead shrike, savannah sparrow [*Passerculus sandwichensis*], lark sparrow [*Chondestes grammacus*], Henslow's sparrow, and Bachman's sparrow probably shifted their nesting requirements to man-made fields after Europeans usurped the natural openings...."

Table 5 (*continued*). Bird species associated with disturbances within forests, especially small (<4 ha) but also for some species larger patches.

Taxon	Watch list[a]	Continental trend[b]	Notes on disturbance-maintained habitat use[c]
Indigo bunting (*Passerina cyanea*)		-* (BBS)	Deciduous forest edge, regenerating sites, open woodlands, second growth, shrubby areas.
Rusty blackbird (*Euphagus carolinus*)		-* (CBC)	Moist woodlands, bushy bogs, wooded edges of water bodies, breeding; forested wetlands, open woodlands, pastures, winter.

[a] Watch List species are identified as in need for conservation attention at the national level (EH = extremely high priority, MH = moderately high priority, M = moderate priority; Carter et al. 1996, 2000).

[b] Continental population trends for this and subsequent tables are mostly from Breeding Bird Survey (BBS, 1966–1999; http://www.mbr.nbs.gov/bbs/bbs.html; Sauer et al. 2000), Christmas Bird Count (CBC, 1959–1988; Butcher 1990), or United States Shorebird Plan (USSP; http://www.Manomet.org/USSCP.htm). Population trends are interpreted following Table 4 in Carter et al. (2000) as follows: -* = significant decrease, - = possible decrease, O = trend uncertain, + = stable or possible increase, +* = significant increase.

[c] Habitat descriptions as they relate to disturbance-maintained conditions are adapted mostly from AOU (1998) or Hamel (1992). Species breed unless otherwise indicated as primarily migrating or wintering in eastern North America.

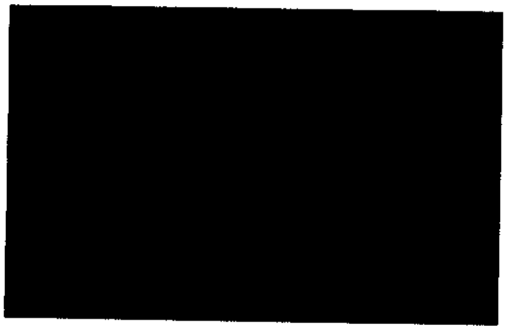
Allowing "nature to take its course" cannot restore the disturbance-maintained ecosystems present prior to European settlement. These conditions are likely lost forever due to the permanent loss of land to human development, loss of keystone species, disruption of natural processes, and an ever-increasing array of exotics (Askins 2000). Nevertheless, we need to understand disturbance-maintained communities and the species dependent upon them so that management strategies can be as effective as the existing science allows.

The key forest bird management issue today lies in how best to protect, create, or restore an appropriate mix of frequently disturbed and infrequently disturbed forested conditions. Given that natural disturbance factors no longer function as they once did, more direct management intervention may be justified from an ecological restoration point of view (Askins 2000). However, restoration should not be at the expense of developing future old-growth conditions in many areas where mid-successional stands now dominate.

Many eastern North American forests today are relatively young (<100 years, Byrd 1996, Trani et al. 2001), such that natural tree mortality resulting in natural forest openings and a long-term series of autogenic regeneration events are almost non-existent. Certainly old-growth conditions for forests not subject to frequent disturbances from storm damage, fire, or grazing are underrepresented compared with pre-European settlement times. Areas dominated by old-growth forest occurred in the expansive forested wetlands of the Southeastern Coastal Plain (including here the Mississippi Alluvial Plain and Peninsular Florida) and in the more sheltered coves of the Appalachians where fire and other disturbance factors were likely rare (Byrd 1996, Delcourt and Delcourt 1997). In time, most likely measured in terms of several centuries, we might expect a return of autogenic regeneration through a return of tree-fall dynamics that should improve the status of most gap-associated species in presently preserved forests (wilderness areas, national parks, etc.).

As an alternative, silvicultural approaches could be used to remedy the present shortage of structural diversity in today's even-aged forests (e.g., Powell et al. 2000, Thompson and DeGraaf 2001). Available data indicate that even-aged silviculture, with at least 100-year rotations in largely forested areas, appears to have little effect on relative abundance of most vulnerable mature forest species, though it provides for greater numbers of early successional species. For example, Thompson et al. (1992) found that some mature forest species occurred in greater numbers in landscapes managed by even-aged silviculture than in passively managed wilderness areas (but not yet supporting old-growth conditions). Thompson (1993) and Annand and Thompson (1997) suggest that in largely forested regions, a combination of uneven-aged and even-aged management may provide stability for mature forest and early successional species.

Evidence is accumulating that early successional habitats also are important for species typically considered to be associated with mature forests (Pagen et al. 2000). For example, fledgling wood thrushes (*Hylocichla mustelina*) move substantial distances (up to 6 km) to seek out patches of disturbance-associated habitats, which may prove critical for providing abundant food resources and protective cover from predators when compared with natal sites dominated in eastern North America today by mid-successional forest conditions (Anders et al. 1998, Vega Rivera et al. 1998). Similar results were found for molting adult wood thrushes in terms of their seeking out "safe havens" where understory cover was denser than around nesting sites (Vega Rivera et al. 1999, Powell et al. 2000). Studies on landbird migration also are demonstrating the importance of larger forest openings to support abundant food resources and protective cover (Kilgo et al. 1999, Suthers et al. 2000).



Cerulean warbler habitat along an old strip-mined contour bench bordering mature mixed deciduous forest in southern West Virginia. Photo by Ronald Canterbury, Concord College, West Virginia.

Proposals to increase managed disturbance also must be integrated with efforts to minimize forest fragmentation effects, including increased depredation and cowbird-parasitism rates, invasions by exotic species, and disruption of natural disturbance processes (especially fire and hydrology). One approach to providing early successional conditions and minimizing fragmentation effects is repeated disturbance to the same stands, therefore minimizing the need to cut other stands as frequently as would be done during a strictly commercial operation (e.g., Litvaitis and Villafuerte 1996). Clearcuts, for example, are most suitable for Henslow's sparrows for 1 to 2 years after harvest and for golden-winged warblers for about 10 years at most (Pruitt 1996, Klaus 1999). Clearcuts followed by one-time management to suppress woody growth might extend the duration of the shrubland condition and thus support an abundance of shrubland birds for 30 years instead of 10 years. Prescribed fire or herbicide treatments may arrest succession and maintain quality grass and shrub communities over longer periods of time than that evident in managed landscapes where such practices are avoided (Schulte and Niemi 1998; Confer, unpublished data).

Negative effects from forest fragmentation (Robbins 1980, Blake and Karr 1987, Robinson et al. 1995) led to defining many Nearctic–Neotropical migrants as "area-sensitive," "forest-interior" dependent, or both. However, area-sensitive and forest-interior are complex, species-specific designations based on habitat relationships that differ depending on the percent of the landscape forested, as well as other site-specific factors. Area-sensitivity also applies to disturbance-dependent species as discussed here (Annand and Thompson 1997). A review by Villard (1998) and meta-analysis by Hartley and Hunter (1998) also suggest that, with respect to forest species, these terms are applied too generally without regard to landscape context (also see Robinson et al. 1995, Donovan et al. 1997).

Largely forested regions, such as the "northern" woods of the Northeast and upper Midwest United States and eastern Canada, the Southern Blue Ridge and Cumberland Plateau of the Appalachians, and the Ozark–Ouachita Highlands, are important for supporting mature forest and disturbance-dependent species. Management decisions may not require close inspection of fragmentation effects as long as forest cover exceeds 70% of the land base, with respect to agriculture and development (Robinson et al. 1995). In more fragmented regions, such as southern New England, the Ridge and Valley within the Appalachians, Shawnee Hills within the Central Hardwoods region, and the Mississippi Alluvial Plain, greater attention must be given to forest patch size. In these areas, segregation of mature forest-dominated habitats is likely necessary from patches that are intended to target grassland and shrub–scrub species (Herkert et al. 1993, 1996; Robinson 1996).

Conclusion

The period of abrupt change from naturally (and culturally) based disturbances to those associated with European and African settlement reached an apex around 1800 along most of the Atlantic Seaboard and Northeast, while they were just beginning in the Appalachians and points westward (Buckner and Turrill 1999). Expansive savannas and prairies described during the 1700s were all but gone by the early 1800s (Noss et al. 1995). After extensive and destructive forest clearing and burning

During winter, high numbers of Henslow's sparrows hide under very dense cover of savanna grasses and forbs at Mississippi Sandhill Crane National Wildlife Refuge, Mississippi. Photo by William Howe, United States Fish and Wildlife Service.

practices in the 1800s, fire suppression policies followed almost unchallenged from the 1930s until the late 1980s. As a result, most disturbance-dependent birds have undergone a cycle of population increases followed most recently (and into the foreseeable future) by decreases in population trends.

Almost all disturbance-dependent birds, regardless of present status, would benefit from returning fire to many of the ecosystems of eastern North America. However, in many areas some level of thinning or mechanical removal of midstory and canopy vegetation may be necessary before fire is reintroduced. In other areas, the details still need to be developed for most effectively implementing fire management for conservation purposes. The role of silvicultural- and grazing-based disturbances also must be considered independent of the use of fire as use of prescribed burning becomes increasingly unpopular or cost-prohibitive in many areas.

Many disturbance-dependent species may in the near future require greater levels of legally based conservation action, such as federal listing, without aggressive restoration of disturbance-maintained communities. Much needs to be learned regarding the most appropriate and responsible approaches to improving forest habitat condition through silviculture and prescribed burning. The future challenge is to conduct necessary management for disturbance-dependent species in eastern North America while balancing the needs of other species of conservation interest associated with older forests not subject to frequent disturbances (see Thompson and DeGraaf 2001).

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Importance of early successional habitat to ruffed grouse and American woodcock

by Daniel R. Dessecker and Daniel G. McAuley

se (*Bonasa umbellus*) and American woodcock (*Scolopax minor*) provide millions of days of recreation each year for people in the eastern United States (U.S). These popular game birds depend on early successional forest habitats throughout much of the year. Ruffed grouse and woodcock populations are declining in the eastern United States as an abundance of shrub-dominated and young forest habitats decrease in most of the region. Continued decreases in early successional forest habitats are likely on nonindustrial private forest lands as ownership fragmentation increases and tract size decreases and on public forest lands due to societal attitudes toward proactive forest management, especially even-age treatments.

Key Words American woodcock, aspen, *Bonasa umbellus*, early successional habitat, even-age management, ruffed grouse, *Scolopax minor*

uffed grouse (*Bonasa umbellus*) and American woodcock (*Scolopax minor*) depend on shrub-dominated and young forest habitats. The high stem densities characteristic of these habitats protect them from predators and enable local populations to attain levels substantially greater than on landscapes dominated by mature forest (Sepik and Dwyer 1982, Gullion 1984*a*). Historically, these early successional habitats were established through periodic disturbance. Fires of aboriginal and "natural" origins were the primary disturbance agents in much of the eastern United States, although insect infestation and wind also affected vegetation structure and composition (Little 1974). Intensity, extent, and frequency of fires varied spatially due to landscape conditions (slope, aspect, etc.). In addition, fire frequency varied temporally in response to changes in climate and changes in Native American population density and distribution (Dessecker 1997, Hamel and Buckner 1998).

The ruffed grouse is the most popular upland game bird throughout much of its range in the eastern United States. Where ruffed grouse populations are cyclic, hunter numbers commonly rise and fall with local populations. During the most recent cyclic high in the late 1990s, approximately 120,000 hunters spent 1,000,000 days afield in each of Michigan, Minnesota, and Wisconsin (Berg 2000, Dhuey 2000, Whitcomb et al. 2000). Total annual ruffed grouse harvest likely approaches 1,000,000 birds in each of these states during the peak of the 10-year cycle. Approximately 300,000 ruffed grouse are harvested annually during cyclic lows.

Ruffed grouse population, hunter effort, and harvest data are scarce outside of the Great Lakes region.

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Gullion (unpublished data) surveyed state resource agencies across the United States and estimated that Maine, New York, and Pennsylvania each harvested approximately 450,000 ruffed grouse in the mid-1980s. Indices of ruffed grouse hunter effort and harvest suggest that both are declining throughout the eastern United States. These data are consistent with survey results documenting a 36% decline in numbers of small-game hunters in the United States between 1985 and 1996 (United States Department of Interior [USDI] 1997).

The American woodcock also is a popular game bird throughout eastern North America. In the 1980s, woodcock provided approximately 3.4 million days of recreational hunting annually (USDI 1990). At that time, U.S. hunters harvested an estimated 1.1 million woodcock annually (Straw et al. 1994), making woodcock among the top 10 species of migratory game birds harvested in the Atlantic and Mississippi flyways. Current estimates of hunter effort and harvest of American woodcock are available from the recently established Harvest Information Program (HIP), although estimates from this survey are imprecise. These data suggest that in 1998–99, 128,000 hunters spent 574,000 days afield and harvested 435,000 woodcock (United States Fish and Wildlife Service [USFWS], Office of Migratory Bird Management [MBMO], unpublished data). States leading in hunter effort and harvest include Louisiana, Michigan, Minnesota, Wisconsin, New York, and Maine.

In this paper we 1) review the current status, recent trends, and factors affecting ruffed grouse and American woodcock populations in the eastern United States; 2) summarize use of early successional habitats by these 2 species; 3) present habitat management recommendations; and 4) discuss the outlook for future trends of these species.

Distribution and status

Ruffed grouse

The ruffed grouse is North America's most widely distributed gallinaceous bird (Johnsgard 1973). Ruffed grouse are found throughout much of the eastern United States, yet are common only where extensive tracts of forest dominate the landscape. Ruffed grouse are common in the northern Great Lakes region and where suitable habitats exist in the Northeast and the central and southern Appalachian Mountains. The southern extreme of the ruffed grouse range coincides with the southern edge of the Appalachians in northeast Georgia. Ruffed grouse are generally rare below 460 m elevation in the southeast portion of their range, although habitats that appear suitable exist in the Piedmont from Louisiana east to Georgia and north through Virginia.

There is no range-wide population survey of ruffed grouse, but some states monitor populations or harvest rates. Male ruffed grouse drum in the spring to attract females. Drumming-male surveys count all males heard in the early morning along 10- or 15-stop routes and can provide an index of local populations (Gullion 1966). Drumming-male densities typically reach 1 to 2 birds/40 ha in the central hardwood forests of the Midwest, the central and southern Appalachians, and in northern hardwood forests in the northern tier of states (Thompson and Dessecker 1997). The aspen (*Populus* spp.) forests of the Great Lakes region can support 4–8 drumming males/40 ha (Kubisiak 1985).

Early successional habitats are by nature ephemeral.

We obtained survey data on trends in drumming males from 5 states: Minnesota (Berg 2000), Wisconsin (Dhuey 2000), Indiana (Backs 2000), Ohio (R. Stoll, Ohio Department of Natural Resources, unpublished data), and Kentucky (J. Sole, Kentucky Department of Fish and Wildlife, unpublished data). These data suggest long-term declines for 3 of these 5 states, though only 2 correlations between grouse abundance and year are significant (Minnesota, r=–0.22, P=0.227; Wisconsin, r=0.04, P=0.824; Indiana, r=–0.89, P<0.001; Ohio, r=–0.727, P<0.001; Kentucky, r=0.61, P=0.143). Hunter flush-rate data (birds flushed/unit of hunter effort) are collected from cooperating hunters in some states. We obtained flush-rate data from Ohio, North Carolina (T. Sharpe, North Carolina Wildlife Resources Commission, unpublished data), Tennessee (M. Gudlin, Tennessee Wildlife Resources Agency, unpublished data), Virginia (Norman 2000), and West Virginia (W. Lesser, West Virginia Department of Natural Resources, unpublished data). Correlations between grouse abundance and year indicate long-term declines for 2 of these 5 states (Ohio, r= –0.454, P=0.03; North Carolina, r=0.297, P=0.38; Tennessee, r=–0.75, P<0.01; Virginia, r=–0.096, P= 0.67; West Virginia, r=0.009, P=0.96). The cyclic nature of ruffed grouse populations in northern latitudes (Figure 1) has been well documented (Keith 1963) and complicates interpretation of trends for these populations.

Woodcock

The American woodcock is a member of the shorebird family that inhabits forested and mixed forest–urban–agricultural areas from Manitoba east to Newfoundland and Labrador and south to Florida, the Gulf of Mexico,

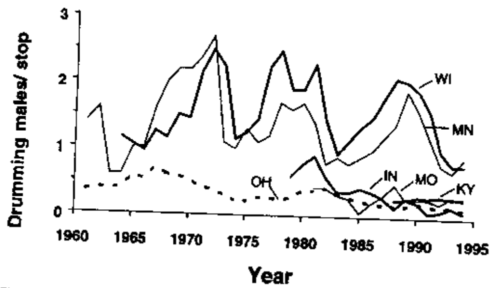

Figure 1. Trends and relative abundance of ruffed grouse based on drumming males heard/stop along multiple-stop survey routes.

and eastern Texas. The northern limit of breeding is indistinct, but may extend to James Bay or southern Hudson Bay (Sheldon 1967, Keppie and Whiting 1994, Straw et al. 1994). In its northern range, the woodcock is one of the earliest ground-nesting species. Woodcock breed most commonly north of 40° N latitude, but there are records of nests in every state and province within its range (Keppie and Whiting 1994). In the south, nesting begins in February, whereas in the north nesting begins in April and May and extends into June or early July (Pettingill 1936; United States Geological Survey, unpublished data).

Woodcock are migratory and winter in southern states where snow cover or ground frost is rare. In the East, Cape May, New Jersey, and Cape Charles, Virginia, are major staging areas for woodcock during migration, especially in fall. Most birds arrive on wintering areas by mid-December (Keppie and Whiting 1994). Areas of high woodcock concentrations recorded during the National Audubon Society's Christmas Bird Count are eastern Texas to central Louisiana, the coastal plain of South Carolina, and the lower Delmarva peninsula to eastern Virginia (Straw et al. 1994).

Woodcock are managed as 2 regional populations, the Eastern and the Central Management Units (Owen et al. 1977). This delineation is justified by band recovery data indicating little crossover of birds between the regions (Martin et al. 1969, Krohn et al. 1974). Reliable indices of population size, productivity, harvest, and distribution of woodcock are difficult to obtain (Bruggink and Kendall 1995). Because of their small size, cryptic coloration, and preference for dense vegetation, it is impractical to census woodcock populations. However, woodcock populations are monitored with the North American Singing-ground Survey (SGS) and the Wing-collection Survey (WCS). In 1968, about 1,500 routes were located randomly across the entire northern breeding range of the woodcock (see Sauer and Bortner [1991] for a review of implementation and analysis of the SGS). The SGS takes advantage of the male woodcock's conspicuous courtship display and provides an index to number of displaying male woodcock present in the population. The surveys count all calling males heard along a 10-stop route that is run after sunset. The short-term (1990–2000) and long-term (1968–2000) trends in both management units are declining (Eastern Unit $r^2=0.926$, $P<0.01$; Central Unit $r^2=0.903$, $P<0.01$ [Kelley 2000]; Figure 2). In the Eastern Management Unit, number of males heard along routes declined at about 2.3%/year since 1968 and by 3.5%/year over the last 10 years. Trends in the Central Management Unit declined 1.6%/year since 1968 and 3.1%/year since 1990.

The WCS is conducted every year in the U.S. and Canada to provide data on reproductive success of woodcock, information on the chronology and distribution of the harvest, and data on hunting success (Kelley 2000). Age and sex can be determined from wing-plumage characteristics (Martin 1964) and the ratio of immature birds/adult female in the survey sample is an index of recruitment. In the U.S. in 1999, recruitment indices in the Eastern (1.1) and the Central (1.2) units were the least on record and were >25% below the 1998 index and >29% below the long-term regional averages of about 1.7 (Kelley 2000). In Canada, the 10-year (1988–97) average recruitment index was 3.1 in Nova Scotia, 2.4 in New

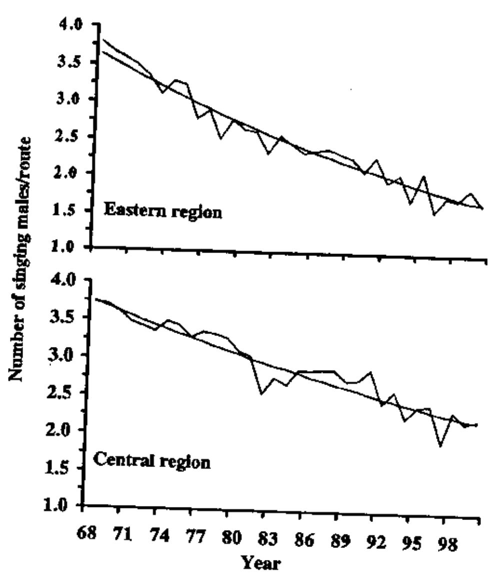

Figure 2. Long-term trends and annual indices of the number of male woodcock heard on the Singing-ground Survey, 1968–2000.

Brunswick, and 1.4 in Ontario. In Canada, the proportion of young in the survey has been declining over the long term (1982–97) in Ontario (P=0.06), whereas changes in Nova Scotia (-) and New Brunswick (+) were not significant (Bateman 1999).

Woodcock harvest is declining in the U.S. and Canada. The estimated harvest in Canada of 45,558 in 1997 was 57% below the 10-year mean (Bateman 1999). In the U.S., estimates of total harvest are imprecise (see Straw et al. 1994), but results of surveys indicate that woodcock harvest and number of woodcock hunters have declined since the early 1980s (Straw et al. 1994, Kelley 2000). Owen et al. (1977) estimated the U.S. harvest at 1.5 million birds; Straw et al. (1994) estimated the harvest in 1991 at 1.1 million, whereas the recent estimates from the HIP survey indicated harvest in 1999 was 435,000 woodcock (USFWS MBMO, unpublished data).

Cause of population declines

Habitat loss and degradation are the predominant factors affecting ruffed grouse and woodcock population trends. Studies suggest that ground-nesting songbirds may currently be experiencing low reproductive rates, possibly due to landscape-level changes in habitat conditions (Robinson et al. 1995). Ruffed grouse and woodcock are ground-nesting birds. Ongoing ruffed grouse research in 7 central Appalachian states has documented relatively high nest success (69%), yet very low chick survival (25%) to age 5 weeks (Appalachian Cooperative Grouse Research Project, unpublished data). Declines in young forest habitats and the isolation of these habitats in some landscapes may be limiting ruffed grouse and woodcock recruitment and therefore population densities.

Habitat use

Ruffed grouse

Ruffed grouse are early successional forest specialists. Optimum habitats for ruffed grouse include young (6- to 15-year-old), even-age deciduous stands that typically support 20–25,000 woody stems/ha (Gullion 1984*a*; Kubisiak 1985; Stoll et al. 1999; Dimmick et al.1998). These habitats are available to grouse for approximately 1 decade because stem densities decrease rapidly through natural thinning as succession proceeds.

Although commonly identified as an "edge" species, ruffed grouse association with habitat edges largely reflects their use of various interspersed forest habitats at different times of the year and their use of marginal edge habitats where quality habitat is lacking. Ruffed grouse typically avoid hard-contrast edges. Gullion (1984*b*:73) states: "...extensive use of forest edges by ruffed grouse provides the best indication of how unsatisfactory a forest habitat has become for these birds."

Ruffed grouse use young stands of many different deciduous forest types throughout North America. However, aspen forests can support ruffed grouse population densities that greatly exceed those attained in other forest communities (Thompson and Dessecker 1997). Regeneration stem densities in recently clearcut aspen stands commonly reach levels that provide excellent protective cover for ruffed grouse. In addition, the dormant flower bud from mature male aspen trees is an important source of food for grouse in winter and early spring.

Young deciduous forest and shrub-dominated old-field habitats protect ruffed grouse from predators throughout the year. Dense stands are especially important to drumming males in spring (Stoll et al. 1979, Boyd 1990).

Habitats used for nesting appear to be variable; nesting hens can be found in a wide variety of habitats, although commonly in forest habitats that are older and more open than those frequented during other times of the year. Ruffed grouse broods are seldom found far from dense cover. Quality brood habitat includes small forest openings with a substantial shrub component. These openings can provide an important source of insects for developing chicks during their first 4–6 weeks of life (Hollifield and Dimmick 1995). Brood habitat is often relatively mesic, typically on north or east slopes in hilly terrain, or in riparian areas (Godfrey 1975, Kubisiak 1978, Thompson et al. 1987).

Ruffed grouse use a wide variety of available foods throughout the year. However, winter food availability and quality may be limiting factors for ruffed grouse populations in the central and southern Appalachians (Servello and Kirkpatrick 1987). In these regions,

American woodcock depend on early successional habitats and moist soils.

The ruffed grouse is the most popular game bird throughout much of the eastern United States.

succulent herbaceous vegetation, typically found on relatively mesic sites, is an important component of ruffed grouse diets.

Woodcock

Habitats used by woodcock vary with activity, time of day, and season, but like ruffed grouse they are an early successional species. They are not restricted to specific plant assemblages (Keppie and Whiting 1994) as long as the habitat provides the necessary early successional structure (Straw et al. 1994). Dense young forest or shrub-dominated habitats on moist soils are ideal (Keppie and Whiting 1994). Moist soils are an important component of quality woodcock habitat as they ensure that earthworms, which comprise nearly 80% of their diet (Sperry 1940), are at or near the soil surface and available to foraging woodcock.

In spring, males need openings called singing grounds to perform courtship displays and attract females for mating. Vegetative composition of singing grounds varies locally and throughout the range and does not likely determine use (Dwyer et al. 1988, Sepik et al. 1993). More likely the quality of the adjacent habitat for nesting and brood rearing determines singing-ground use by males. At night during summer, many birds use clearings, such as blueberry (*Vaccinium* spp.) barrens, pastures, recently harvested woodlands, and plantations, for roosting (Dunford and Owen 1973, Sepik et al. 1981, Sepik and Derleth 1993). Many of these same fields are used for singing grounds in spring.

Woodcock nest in a variety of habitats. Nests and broods are found in young to mixed-age forests, although they prefer young hardwood stands (Mendall and Aldous 1943), especially aspen (Gregg and Hale 1977, McAuley et al. 1996). Typically, numbers of trees >7.6 cm diameter (400–783/ha) and basal area (6–9.5 m^2/ha) are low, whereas density of saplings <7.6 cm (1,400–4,500/ha) and shrubs (13, 500–49,250/ha) is high (Bourgeois 1977, Coon et al. 1982, Parris 1986, Kinsley and Storm 1988, McAuley et al. 1996).

During summer, young hardwoods or older stands with a dense understory, particularly alder (*Alnus* spp.), provide daytime cover for feeding (Morgenweck 1977, Rabe 1977, Hudgins et al. 1985). In northern breeding areas, conifer stands are used rarely, except during drought when they may be critical for survival (Sepik et al. 1983). Diurnal habitats in fall and on migration are young hardwood stands on moist soils with dense shrubs (Keppie and Whiting 1994).

In winter, a variety of habitats are used diurnally, especially bottomland hardwoods, upland mixed pine–hardwoods, and recently burned stands of longleaf pine (*Pinus palustris*), although young hardwood stands are preferred (Glasgow 1958, Britt 1971, Dyer and Hamilton 1977, Krementz and Pendleton 1994). In pine stands, preferred microhabitats include depressions or drainages dominated by deciduous species. Mature stands of bottomland hardwoods are used if the canopy is sufficiently open to allow an understory of saplings, vines, and forbs to develop (Roberts et al. 1984). In Louisiana, Dyer and Hamilton (1977) reported that bottomland hardwoods used by woodcock contained dense stands of small-diameter trees. Kroll and Whiting (1977) in eastern Texas found substantial woodcock use of 2-year-old clearcut pine stands and pole-sized mixed pine–hardwood stands that had a high basal area of pine and abundant deciduous shrubs. Causey (1989) reported high variability in habitats used by woodcock, yet most stands had a well-developed shrub understory.

Habitat management

Ruffed grouse

Early successional habitats are by nature ephemeral. On landscapes where it is impractical to allow the return of natural fires or introduce prescribed fires, commercial timber harvests and other proactive habitat management practices must be implemented at regular intervals (approximately every 10 years) to ensure a continuous supply of quality ruffed grouse habitat on the landscape. Forest types that reach biological or economic maturity more rapidly can be managed using shorter rotations, thereby increasing amount of ruffed grouse habitat that is available on the landscape at any one time. Reductions in the proportion of a management unit where forest management is practiced can reduce ruffed grouse habitat potential.

Even-age silvicultural systems (clearcut, seed tree, shelterwood) are the most appropriate methods to create ruffed grouse habitat. These methods remove sufficient canopy from the parent stand to result in enough understory development to provide protective cover for ruffed grouse. Group-selection treatments can produce stem densities comparable to clearcut regeneration harvests (Weigel and Parker 1995), but patch sizes are generally too small to provide secure cover for ruffed grouse. Selection methods may be beneficial in riparian areas or other areas where understory development is desired yet even-age management is precluded.

Regeneration harvests that retain low levels of residual basal area are called clearcut with reserves, modified shelterwood harvests, or deferment cuts. In general, the greatest amount of overstory removal will yield the greatest degree of understory development. Retention of a limited number of residual trees may not affect regeneration stem densities in developing stands. Smith et al. (1989) found similar stem densities 5 years post-treatment in clearcut central hardwood stands and stands with <4.9 m^2/ha of residual basal area. Aspen is extremely shade-intolerant. Perala (1977) showed that as little as 2.5–3.7 m^2/ha of residual basal area can reduce aspen regeneration growth by 40%. Residual basal areas of 2.5 m^2/ha can reduce aspen regeneration stem densities after the first growing season by 29% (D. M. Stone , United States Forest Service [USFS], unpublished data).

The diameter distribution of residual trees also can significantly affect regeneration stem densities. For example, retaining approximately 16 38-cm-diameter trees or 150 12.5-cm-diameter trees provides 2 m^2 of residual basal area. Although the crowns of the larger-diameter trees are more expansive than those of the 12.5-cm trees, the latter would quickly respond to release. The shade cast by the combined crowns of these small-diameter trees could have a greater effect on the developing regeneration than would the shade cast by the larger trees.

The spatial distribution of residual trees within a harvest unit also can significantly affect regeneration stem densities. Residual basal area maintained in discrete patches will minimize shading of regenerating hardwoods and therefore effects of this shade on regeneration stem densities. Residual basal areas >4.9 m^2/ha can reduce regeneration stem densities and should not be maintained within harvest units designed to provide quality habitat for ruffed grouse (Thompson and Dessecker 1997). In addition, residual basal area levels <4.9 m^2/ha in aspen and other shade-intolerant forest types can reduce stem densities and habitat quality for ruffed grouse (Perala 1977).

Research in aspen forests managed on a 40-year rotation shows that small harvest units (1–2 ha) are more beneficial to ruffed grouse than larger harvest units (Gullion 1984*a*). The small harvest units are designed to provide ruffed grouse with patches of protective cover (6- to 15-year-old stands) interspersed with mature stands that provide male flower buds for grouse during winter. In other forest types managed using longer rotations (60–100 years), ruffed grouse can benefit from habitat interspersion, but they may not benefit from a pattern of small-block timber harvests to the same degree as in aspen forests. Scattered small-block harvest units on landscapes dominated by mature forest can provide patches of habitat for ruffed grouse, but these isolated islands likely provide only limited security from predators.

Woodcock

Habitat management beneficial to ruffed grouse generally benefits woodcock. However, because woodcock feed primarily on earthworms and other invertebrates, soil moisture and fertility, slope, aspect, and other site factors must be considered (Sepik et al. 1981, Roberts 1989). Habitat management in valleys and lower slopes is more beneficial to woodcock than management on dry upper and middle slopes (Liscinsky 1972). McAuley et al. (1996) recommended maintaining ≥25% of a unit in early successional habitat through clearcutting blocks >2 ha, or cutting 30-m-wide strips in mature forest on about a 40-year rotation. Stands of alders and similar moist-soil shrub species should be encouraged and maintained by cutting strips on a 20-year rotation across moisture gradients. Blueberry fields can be maintained through periodic burning, and fields and pastures can be maintained by mowing either completely or in strips.

On wintering areas, burning, mowing, herbicide application, tillage, and timber harvest can be used to create or maintain habitat for woodcock. Regeneration created by clearcutting small blocks provides excellent woodcock cover, although selective cutting also can be beneficial (Roberts et al.1984). Thinning pole stands can benefit woodcock by encouraging development of midstory and understory vegetation. Mature stands can be maintained in good woodcock cover by removing sufficient overstory canopy to allow light to reach the ground and promote dense shrub layers. Seed tree and shelterwood cuts also are beneficial silvicultural treatments.

Feeding is presumed to be a primary reason woodcock use roosting fields in winter. Pastures and fallow fields can be burned to remove dense vegetation, which will make them more attractive to woodcock for nocturnal roosting (Glasgow 1958). Mowing strips and patches in fall after growth has ceased can help create foraging areas for woodcock (Krementz and Jackson 1999). Brief periods of intense grazing by livestock can be used to set back plant succession and enhance use by woodcock, although intensively grazed fields that result in extensive areas of very short grass will receive little use (Krementz and Jackson 1999).

Pine plantations <3 m tall are used by woodcock, but once the canopy closes and shrub densities decline, they are not often used (Krementz and Pendleton 1994). Thinning closed-canopy stands so that light can reach the forest floor allows thickets of hardwood seedlings, blackberries (*Rubus* spp.), switch cane (*Arundinaria tecta)* and other plants to grow under the pines. Clearcuts provide nighttime habitat and also, within a few years, daytime cover. Shelterwood and seed-tree harvests create patches of suitable woodcock habitat, but they also provide roost sites for birds of prey (Krementz and Jackson 1999). Clearcutting small blocks in stands of bottomland hardwoods provides excellent woodcock cover (Roberts et al. 1984).

Likely future trends

The long-term declines in ruffed grouse and woodcock populations are likely the result of the degradation and loss of suitable early successional habitats (Owen et al. 1977, Dwyer et al. 1983, Straw et al. 1994, Thompson and Dessecker 1997). Habitat loss has been associated with urbanization, especially in the mid-Atlantic states, forest succession on the northern breeding areas, and drainage and land-use conversion on the wintering grounds (Straw et al. 1994).

To provide quality habitat for ruffed grouse and woodcock, timber harvest and other forest disturbance should remove sufficient basal area and stems from a stand to allow understory development. Timber harvest practices commonly used in the eastern United States leave residual basal areas that exceed the levels necessary to allow development of quality understory habitat. Guidelines to manage forested riparian areas that, *a priori*, preclude removal of substantial overstory vegetation may unnecessarily limit development of early successional habitat on these sites, which could provide important resources for ruffed grouse, woodcock, and other early successional wildlife. During the interval between the 2 most recent forest inventories (early 1970s to mid-1980s), more than 60% of the basal area was removed from only 4% of the forest stands in West Virginia and from 8% of the stands in New England (Gansner et al. 1990, Birch et al. 1992). On most sites, removal of <60% of the basal area is not adequate to establish quality habitat for ruffed grouse and woodcock.

Only 14% of the timberland in the eastern United States is in public ownership (Powell et al. 1993). Public land management agencies have responded to public concerns over proactive forest management by proposing significant reductions in levels of timber harvest and in the prescription of even-age regeneration methods (USFS 1995). Approximately 70% of the timberland in the eastern United States is in non-industrial private (NIPF) ownership. Birch (1996) reported that privately owned forest tracts <40 ha in size increased from 12.3 million ha (26.7% of private forest land) in 1978 to 22.9 million ha (43.6% of private forest land) in 1994. As the size of NIPF tracts decreases, so does the likelihood of timber harvest activity (Birch 1986, Roberts et al. 1986).

The forests of the East are maturing. New England forests currently are dominated by saw timber-sized trees, whereas the early successional seedling–sapling stands that woodcock and ruffed grouse require are becoming regionally scarce and as of 1988 composed only 8% of the timberland in the Northeast (Brooks and Birch 1988). This trend is consistent throughout much of the East (Trani et al. 2001). Declines in young forest are the result of changing management objectives and techniques, changing attitudes of landowners, a decline in farm abandonment, increased fire suppression, and increased urbanization (Brooks and Birch 1988, USFWS 1996). Societal attitudes toward timber harvest may continue to limit efforts to provide early successional habitats, thereby exacerbating the ongoing declines of ruffed grouse, American woodcock, and other wildlife dependent upon young forest habitats.

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Importance of early successional habitats to mammals in eastern forests

by John A. Litvaitis

of mammals that depend on early successional forests or shrub-dominated declining in portions of the eastern United States. Although much of this be attributed to maturation of young forests that once dominated the East, on and suppression of natural disturbances also have been implicated. Responses by habitat specialists (e.g., New England cottontails [*Sylvilagus transitionalis*]) and carnivores with large area requirements that rely on prey associated with early successional habitats (e.g., bobcats [*Lynx rufus*]) have been most extreme. Populations of facultative or opportunistic users of early successional habitats (e.g., black bears [*Ursus americanus*] and little brown bats [*Myotis lucifugus*]) apparently have not been affected by fewer young stands. As eastern forests mature, biotic and abiotic forces will increase abundance of early successional habitats. However, maturation of these forests will take a century or more. In the meantime, using even-aged silviculture and applying controlled burns to native shrublands may be useful to alleviate current shortages. In landscapes modified substantially by suburban-urban developments and dense networks of roads, conventional management efforts likely will be insufficient. In these regions, increased populations of generalist predators are capable of exerting intense predation on mammalian herbivores that are restricted to small patches, and movement between patches by small mammals is limited. Mammals with large area requirements also are hampered in these landscapes by frequent road crossings. These limitations may require implementing habitat management programs for mammals that differ from those developed for other disturbance-dependent taxa. Large (>10-ha), clustered patches of early successional habitat may be necessary to maintain viable populations. The effectiveness of these managed habitats will be further enhanced by positioning them close to existing land uses that are characterized by early successional habitats (e.g., powerline corridors). In agricultural landscapes, the representation of old-field habitats could be increased in set-aside programs.

Key Words bats, black bears, bobcats, cottontails, disturbance, early successional habitat, mammals, snowshoe hares

ammals are often overlooked as indicators of habitat change because many species are secretive, occur at low densities, or have generalized lifestyles that are satisfied by numerous habitats. These characteristics may limit ability of natural resource managers to track any relationship between mammal abundance and habitat change. Despite these limitations, mammals respond to natural disturbances (e.g., MacMahon et al. 1989) and human

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land uses (e.g., Kirkland 1977) that alter habitat structure and ecological succession. In eastern forests, this response includes a fairly predictable succession of species that colonize a site as it progresses from grassy clearing to closed-canopy forest (Beckwith 1954, Golley et al. 1965). Depending on the region, meadow voles (*Microtus pennsylvanicus*) or oldfield mice (*Peromyscus polionotus*) are among the first to colonize abandoned fields (Beckwith 1954, Golley et al. 1965). As a woody understory develops, cottontails (*Sylvilagus*) or snowshoe hares (*Lepus americanus*) begin to occupy the site (Beckwith 1954, Burgason 1977). Eventually squirrels (*Glaucomys, Sciurus*, and *Tamiasciurus*) become residents as trees dominate the area (Wilson and Ruff 1999). Clearly, this sequence is a simplification of the habitat associations of mammals, but it does indicate that forests with a variety of seral stages will support a diverse mammal community (Hunter 1990).

Land-use patterns have had an obvious influence in shaping the age structure of eastern forests for centuries (Williams 1989, Lorimer 2001) and thus have affected the historic and current composition of forest wildlife communities (Litvaitis 1993, McWilliams et al. 1997). In portions of this region, early successional forests and shrub-dominated habitats are becoming increasingly scarce (Litvaitis et al. 1999, Trani et al. 2001). Seedling– sapling stands currently represent the smallest portion of forestlands in northeastern (e.g., Massachusetts: 4%) and north-central (e.g., Illinois: 3%) states (Trani et al. 2001). This compares to substantially larger amounts of young forests in other areas, especially the Coastal Southeast (e.g., seedling–sapling forests represent 35% of timberlands in Alabama and Mississippi, Trani et al. 2001). Populations of mammals associated with young forests also are declining in northeastern (Litvaitis 1993) and north-central states (Mankin and Warner 1999*a*). Although the ramifications of these declines on regional biological diversity are not understood completely, long-term viability of some species may be in jeopardy (Litvaitis and Villafuerte 1996). This situation warrants conservation attention now.

Approximately 140 species of mammals are native to the eastern United States, and about 90 of these are associated with forested habitats (estimated from Wilson and Ruff 1999). In this paper, I examine the relationships of forest mammals to shrub-dominated and disturbance-generated habitats in the eastern United States. First, I differentiate between species that are responsive to changes in the abundance of these habitats and those that simply utilize them opportunistically. Next, I consider other factors that limit the suitability of early successional habitats to mammals in many contemporary landscapes. Finally, I describe approaches to manage disturbance-generated habitats in regions where these communities are in short supply and how management efforts can be placed in a landscape context to maximize their suitability to mammals.

Perhaps a logical first step in considering how to respond to reductions in early successional habitats would be to define an appropriate benchmark or baseline for comparison. If we could decide on the "normal" abundance of these habitats, then we should be able to respond to a shortfall or overabundance rather than simply react to changes.

Responses by mammals to forest disturbances

Early successional obligates

Among the mammals that depend on young forests or shrub-dominated communities in the eastern United States, lagomorphs may be the most widespread group. Cottontails and snowshoe hares occupy a variety of habitats in this region (Wilson and Ruff 1999), but local abundance depends on availability of dense understory vegetation (e.g., Litvaitis et al. 1985, Barbour and Litvaitis 1993).

In the Northeast, New England cottontails (*Sylvilagus transitionalis*) occupy wetlands, idle agricultural lands, powerline corridors, and patches of regenerating forest (Litvaitis 1993). In these habitats, secondary succession has progressed approximately 10–25 years and understory vegetation provides food and cover (Barbour and Litvaitis 1993). As trees on these sites mature and understories thin, local cottontail populations decline rapidly (Figure 1*a*). Historically, New England cottontails likely occupied native shrublands associated with rocky outcrops or wetlands and forests regenerating after a small-scale (e.g., inundation by beavers [*Castor canadensis*], lightning strike, or windthrow) or large-scale (e.g., hurricanes, wildfires, or fires intentionally set by native peoples) disturbance. Clearing of forests for agriculture by European settlers and subsequent abandonment of these lands was an extreme disturbance event that profoundly affected the abundance of early successional habitats (Litvaitis 1993). New England cottontails and other early

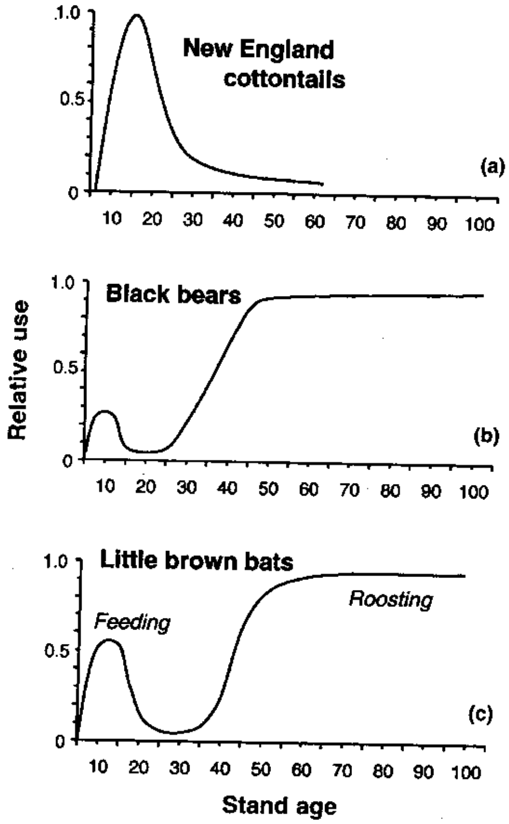

Figure 1. Conceptual representation of seral-stage associations of several mammals in eastern forests. New England cottontails (a) are considered obligate users of young stands because these habitats provide all food and cover needs. Black bears (b) are consider opportunistic users of young stands, and mature stands are used in all seasons. Little brown bats (c) also can be considered opportunistic users of young stands. Bats may congregate in these stands, but the stands do not contain a greater concentration of insects, and bats also forage in other habitats. Mature stands are used as diurnal roosts, and abundance of roosts may limit suitability of a forest to bats. Response curves were adapted from Giles (1978).

successional vertebrates reached unprecedented levels of abundance in the Northeast during the late 1800s and early 1900s (Litvaitis 1993). However, most of these abandoned farmlands matured into closed-canopy forests (circa 1960), and populations of New England cottontails and other taxa quickly retracted. Currently, populations of cottontails are small, disjunct, and span approximately 20% of the area this species occupied historically (Litvaitis and Litvaitis 1996). In response to this decline, the Northeastern Nongame Technical Committee has listed the New England cottontail as a priority species for additional restoration efforts and several national organizations have petitioned the United States Fish and Wildlife Service to list this species as threatened or endangered (M. Amaral, United States Fish and Wildlife Service, Concord, N.H., personal communication).

In the Mid-Atlantic and Interior Southeast, Appalachian cottontails (*S. obscurus*, previously considered southern populations of *S. transitionalis*, see Chapman et al. 1992) occupy a variety of early successional forests with dense shrubs (especially *Rubus*) or mature stands with a dense understory of rhododendron (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), or blueberries (*Vaccinium*) at high elevations (ca. 700–900 m above sea level, Sommer 1997). In western Maryland, for example, Appalachian cottontails selected sites within 2 m of dense understory vegetation and avoided sites with sparse understory cover (Sommer 1997). Although only limited research has been conducted on the historic and current abundance of this species, populations have declined (Merritt 1987) in response to habitat fragmentation and suppression of wildfires (Chapman and Morgan 1973, Sommer 1997). Remaining populations are currently restricted to large blocks of continuous forests where human land uses are limited (Chapman and Stauffer 1981, Chapman et al. 1992).

Eastern cottontails (*S. floridanus*) occupy the largest geographic range of any cottontail (Chapman et al. 1982) and are adapted to exploit a variety of habitats, including those modified by contemporary land uses (Smith and Litvaitis 2000). Nevertheless, this species also has responded to changes in land use. Initially, clearing forests for agriculture resulted in an interspersion of fields, brushy edges of pastures, and woodlots that provided eastern cottontails with abundant food and cover, and populations expanded (Chapman and Morgan 1973). However, subsequent changes in agricultural practices (especially in the Midwest) have reversed this trend. For example, farming practices in Illinois have shifted to large fields that are dedicated to single crops, and idle areas and hedge rows have been cleared (Vance 1976, Mankin and Warner 1999*a*). Populations of eastern cottontails there declined by >70% from 1956 to 1978 in response to these changes (Mankin and Warner 1999*a*). Although eastern cottontails are able to persist in these intensively farmed areas, they are substantially restricted to small portions of the landscape where suitable cover is available (Mankin and Warner 1999*b*). Remaining shelterbelts and other woody vegetation associated with farmsteads provide the only cover, which is critical to cottontail survival in winter (Mankin and Warner 1999*b*).

I have highlighted responses of lagomorphs to losses of early successional forests and shrub-dominated habitat because these species obviously depend on these habitats. Additionally, lagomorphs are significant components in many biotic communities, and changes in abundance of these herbivores influence other trophic levels (e.g., Wagner 1981, Boutin et al. 1995). For example, rabbits or hares are the major prey of bobcats (*Lynx rufus*) throughout the range of this carnivore (Larivière and Walton 1997). The decline of New England cottontail populations resulted in functional and numeric responses among bobcats in the Northeast (Litvaitis 1993). Specifically, cottontail remains were found in 43% of the bobcat carcasses that were submitted for bounty payment during 1951–1954 in New Hampshire. This dropped to an occurrence of only 10% in carcasses collected during 1961–1965, the period when second-growth forests were no longer suitable for New England cottontails (Litvaitis 1993). Likewise, average annual harvests of bobcats by trappers and hunters in New Hampshire dropped from 350 in 1951–1954 to only 36 during 1965–1969 (Litvaitis 1993). Abundance of bobcats in New Hampshire apparently has not rebounded despite closed hunting and trapping seasons for >15 years (E. Orff, New Hampshire Fish and Game, Durham, N.H., personal communication).

Facultative or opportunistic users of early successional forests

Most mammals that occupy eastern forests utilize resources from 2 or more habitats on a daily or seasonal basis (DeGraaf and Yamasaki 2001). For example, black bears (*Ursus americanus*) utilize numerous seral stages in response to the seasonal distribution of food (Pelton 1982). In spring, grasses, forbs, and buds are important foods. These are abundant in wetlands, forests openings, and regenerating stands (Landers et al.1979, Pelton 1982). These same areas also contain soft mast-producing shrubs (e.g., *Rubus*, *Vaccinium*, and *Gaylussacia*) that are consumed by bears in summer (Brody and Stone 1987). Depending on the forest type and geographic region, bears may not depend on regenerating stands in spring and summer because foods used in these seasons are found in older stands or other habitats (e.g., Lander et al. 1979). Clark et al. (1994), for example, reported that transmitter-equipped bears in Arkansas used regenerating stands less than expected even though these sites had abundant seasonal foods.

In late summer and autumn, bears move to mature stands of oak (*Quercus* spp.), hickory (*Carya* spp.), black gum (*Nyssa sylvatica*), or beech (*Fagus americana*), where they consume the hard mast or seeds of these trees (Landers et al. 1979, Pelton 1982). Although spring and summer foods maintain bears during these seasons, the high concentration of carbohydrates and fats in hard mast have an obvious influence on bear survival and reproduction (Rogers 1976). As a result, mature forest stands are more influential than regenerating stands in affecting productivity of a local bear population (Figure 1*b*).

Bats also utilize a variety of habitats and forest size-classes (Barclay and Brigham 1996, Pierson 1998). In the Northeast, little brown bats (*Myotis lucifugus*) forage in a variety of habitats (e.g., over bodies of water and forest trails) and roost in mature forests or human-built structures (Anthony and Kunz 1977, Krusic et al. 1996). In one predominantly forested landscape, little brown bats were detected foraging in regenerating stands more often than any other seral stage (Figure 1*c*, Krusic et al. 1996). Foraging bats may indeed congregate in regenerating stands, but insect abundance in these stands is no greater than in older stands (Grindal and Bringham 1998). Roosting sites may be more limiting than foraging habitat to little brown bats and other forest-dwelling bats (Pierson 1998).

It is apparent that bears and bats utilize early successional habitats, but the resources sought by both taxa in young forests are available in other seral stages or non-forested habitats. As a result, we should not expect an obvious numeric response to the decline in early successional habitats by either species. Responses by other opportunistic users of these habitats may differ. White-tailed deer (*Odocoileus virginianus*) utilize early successional forests, and these areas often provide more forage than older forest age-classes (Harlow 1984: Figure 112). Deer can respond to the availability of these habitats at local and regional scales (Harlow 1984). Following widespread timber harvesting in the Great Lakes region, deer populations increased from approximately 2–4/km^2 to about 14/km^2 (Alverson et al. 1988). Notwithstanding this response, deer should not be considered early successional obligates. This generalist species is even more responsive to human-dominated landscapes. For example, deer densities have exceeded 50/km^2 in portions of Pennsylvania where woodlots, pastures, and croplands combined to provide deer with an abundance of forage and cover (Palmer et al. 1997).

Limitations of early successional habitats in contemporary landscapes

As mid-succession forests throughout the East mature, natural forces will eventually generate disturbances in which understory vegetation can develop. However, it likely will be a century or longer before these stands reach a size- and age-class distribution where disturbances create openings on a regular basis (Borman and Likens 1979). Most of these openings will be small, several hectares or less (Lorimer 2001). In pre-colonial landscapes, such openings were important habitats for disturbance-dependent mammals. The matrix that now comprises many eastern landscapes, however, is very different from historic conditions (including agricultural fields, suburbs, industrial parks, and extensive networks of powerlines and roads). Small disturbed patches may no longer function as suitable habitat in these altered environments. The current condition of New England cottontails and bobcats illustrates this point.

New England cottontails that occupy small (<3-ha) patches of habitat encounter food shortages during winter (Villafuerte et al. 1997). In response, cottontails in small patches frequently forage away from escape cover and are killed by predators at approximately twice the rate as cottontails on large patches where per-capita food resources are more abundant (Barbour and Litvaitis 1993, Villafuerte et al. 1997). It may seem counter to previous comments on the decline of bobcats to suggest that predation can be influential in limiting cottontails. Generalist predators (especially coyotes [*Canis latrans*] and foxes [*Vulpes vulpes*]) that are capable of exploiting a variety of habitats and prey, however, have replaced bobcats as the major proximate mortality factor of cottontails (Barbour and Litvaitis 1993, Smith and Litvaitis 2000). Populations of these predators have increased in response to converting forests to other land uses (Oehler and Litvaitis 1996). Thus, as cottontail populations have declined in response to habitat loss, their predators have increased. Survival rates of cottontails in small patches are so low that these patches function as demographic sinks (Barbour and Litvaitis 1993, Brown and Litvaitis 1995, Villafuerte et al. 1997). As a result, the pattern of local extinction and subsequent recolonization that likely characterized populations of New England cottontails in pre-Columbian landscapes is no longer viable. Few individuals disperse from small patches of habitat (Barbour and Litvaitis 1993), and those that do encounter habitats with limited cover where they are vulnerable to intense predation (Brown and Litvaitis 1995). Present-day populations of New England cottontails, therefore, are dependent on large patches of habitat close to each other to assure long-term survival (Litvaitis and Villafuerte 1996).

Bobcats also are at risk in some eastern forests. Home-range size of bobcats was correlated with local abundance of lagomorphs (Litvaitis et al. 1986). As a result, scarce or widely disjunct prey populations may result in frequent road crossings by bobcats, making them vulnerable to vehicle collisions and other sources of mortality. Collisions with vehicles were the second most frequent cause of mortality among a group of transmitter-equipped bobcats in Maine (20% of all mortalities, Litvaitis et al. 1987) and likely affect regional distributions of this carnivore (*sensu* Fuller et al. 1992). These observations indicate that efforts to benefit mammals may vary according to the degree that regional land uses have modified forest continuity.

Managing early successional habitats to benefit forest mammals

Perhaps a logical first step in considering how to respond to reductions in early successional habitats would be to define an appropriate benchmark or baseline for comparison. If we could decide on the "normal" abundance of these habitats, then we should be able to respond to a shortfall or overabundance rather than simply react to changes. Such a discussion would be especially relevant when considering how to manage habitats where the influences of contemporary human populations are limited or can be controlled and where disturbance regimes can operate to recreate baseline conditions.

Management in landscapes with limited human activity

In regions where forests remain largely intact, the resumption of natural disturbances may eventually generate sufficient habitats to sustain populations of early successional mammals. Public lands, especially national forests, may be large enough to avoid concerns of generalist predators and networks of paved highways. As a starting point, the amount of early successional habitat could be based on historic (pre-Columbian) levels of disturbance. This will obviously vary by forest type and region (e.g., Lorimer 1977, Ware et al. 1993). Management activities (including even-aged timber management) could then be used to complement existing spatial and temporal scales of disturbance. The level of human intervention would be based on the degree that natural disturbances are affecting forest age-class distribution relative to baseline conditions. In mid-successional forests, human intervention may be essential in providing sufficient habitat for decades until natural disturbances are sufficiently frequent.

Regardless of the specific manipulations used (e.g., Thompson and DeGraaf 2001), management activities will require public support, which is currently lacking. Public opposition to activities that create and maintain early successional habitats (especially clearcutting) is responsible for the obvious reluctance by the United States Forest Service to achieve its mandated objectives of providing these habitats on several eastern forests (Litvaitis et al. 1999). The recent decision to list Canada lynx (*Lynx canadensis*) as a threatened species (Nordstrom et al. 2000), however, should stimulate new discussions regarding habitat management on northeastern and north-central forests. The United States Fish and Wildlife Service and United States Forest Service recently developed a lynx conservation agreement (United States Forest Service Agreement #00-MU-11015600-013) that requires the Forest Service to promote the conservation of lynx habitat on national forests within the historic range of lynx. Because the demography of lynx is closely associated with abundance of snowshoe hares (Ruggiero et al. 2000), application of even-aged timber management may increase (from near nonexistent levels on some forests) to assure an adequate prey base. Concern for populations of other species (especially migratory songbirds, Hunter et al. 2001) may prompt similar discussions in other regions.

Although the creation of early successional habitats in much of the East has been associated with even-aged timber management, this is not essential in some areas, especially on xeric sites. Disturbance-dependent habitats also include pitch pine (*Pinus rigida*) and scrub oak (*Quercus ilicifolia*) barrens. These habitats have been degraded and reduced substantially throughout the eastern United States in response to various land uses and the suppression of wildfires (Motzkin et al. 1999). Restoration of these communities can provide substantial habitat but will require more than simply cutting existing vegetation (Niemuth and Boyce 1998). Once located, candidate sites should be prioritized based on several criteria, including land-use history and the ability to reinstate burning regimes. Sites that have never been plowed may support more diverse communities (Motzkin et al. 1999) and should be favored.

Management in human-dominated landscapes

In regions where the continuity of forests has been disrupted by intense human activity, innovations in habitat management will be needed to provide suitable habitat. Here, natural disturbance patterns (i.e., many small and few large disturbances) may not provide a useful template because of the limitations imposed by a fragmented landscape. Diverse land uses, small average land holdings, and frequent turnover in land ownerships also will present challenges to manipulating forest habitats (Brooks and Birch 1988).

In landscapes substantially modified by suburban–urban developments with a dense network of roads, it may be most effective to dedicate moderate (>10-ha) to large (>25-ha) tracts to serve as "core habitats." These tracts could support populations of small herbivores that would be less susceptible to the limitations of the surrounding landscape matrix and large enough to withstand short-term perturbations. Clustering core habitats (within several kilometers of each other) and positioning them adjacent to existing land uses that include early habitats (especially powerline corridors [Askins 1994]) would facilitate exchanges among populations of small mammals and other vertebrates associated with early successional habitats (Kjoss and Litvaitis 2001). Powerline corridors may function as dispersal corridors that link 2 or more clusters of habitat within a township, thus promoting regional security. Maintaining clusters away from paved roads also would maximize their suitability to wide-ranging carnivores (Litvaitis et al. 1996). If suitable public lands are not available to serve as core habitats, conservation easements may be necessary to assure long-term commitment. Maintaining these habitats with timber harvests may not be cost-effective. Mowing and selective use of herbicides (Thompson and DeGraaf 2001) may be the most practical alternatives to prevent an overstory canopy from developing. If management schedules permit, including these sites in the regular maintenance of adjacent powerline corridors would reduce costs.

In agricultural areas, development of new federal set-aside programs has the potential to provide additional habitats. In recent decades, programs such as the Conservation Reserve Program (CRP) have diverted considerable lands from production agriculture back to native habitats (Warner et al. 2000). Most of these programs were directed toward grasslands, and the benefits to wildlife in these habitats were substantial (Reynolds et al. 1994). Although CRP contracts lasted 10 years, most agreements (e.g., Payment-In-Kind and Acreage Conservation Reserve) were short-term (often annual). Such arrangements have limited effects on improving habitat (Warner et al. 2000) and would do nothing to enhance early successional forests. If these programs are re-established, modifications of contract length and the variety of habitats eligible for enrollment could substantially restore habitats with native shrubs and trees to areas of the Midwest.

Obviously, the scenarios just described are hypothetical, but they do suggest that it is possible to provide suitable early successional habitats in substantially modified ecosystems. Such efforts would substantially improve the status of mammals and other wildlife dependent on these habitats.

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Human dimensions of early successional landscapes in the eastern United States

by Paul H. Gobster

teractions with early successional landscapes are varied and diverse. I review key ways that people perceive, use, and value forest landscapes, emphasizing selected types of early successional landscapes in the eastern United States (U.S.): production and consumption of timber and nontimber forest products, visual and aesthetic perceptions, and recreational uses and choices. Site- and regional-scale forest planning and design efforts can be improved by better understanding the human dimensions of early successional landscapes, such as siting facilities for recreation and planting native vegetation for aesthetics. Various types of communication, such as signs, brochures, and opportunities for on-the-ground experience, can help interpret the significance of these landscapes to the public for wildlife and human values. I suggest some research directions to increase knowledge about the human dimensions of early successional landscapes.

Key Words aesthetics, early succession, forest products, perceptions, recreation

n this paper I discuss the human dimensions of early successional landscapes in the eastern U.S. Human dimensions is a commonly used term to describe the range of perceptions, attitudes, values, uses, and other interactions that people have toward something such as wildlife (e.g., Gray 1995). In the natural resources field this term often centers on questions about management. I use the term landscape rather than habitat because the former conveys more clearly how people perceive and relate to the land (but see my discussion of "recreation habitats" later). Etymologically, landscape is the land that is scoped by a person, that which surrounds and is comprehended (Rolston, in press). Landscapes such as prairies thus might be comprehended as habitats or ecosystems but might also be understood as places defined by their aesthetic characteristics or cultural–historic meanings (Naveh 1995). Early successional refers to landscapes that exist through periodic natural or human-caused disturbance to favor young stages of forest growth such as aspen (*Populus* spp.) saplings; grasses, forbs, or shrubs such as a tallgrass prairie or alder (*Alnus* spp.) thicket; and those with scattered overstory trees such as an oak (*Quercus* spp.) savanna or pine (*Pinus* spp.) barrens (Curtis 1971).

Early successional landscapes in the eastern U.S. are diverse in their structure, function, and composition of plant and animal species. Consequently, it is difficult to characterize generally how such places and their wildlife might be perceived and used by humans. Research is especially sparse on the human dimensions of any particular

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early successional landscape; most studies examining people's production and consumption of forest products, visual and aesthetic perceptions, recreational uses and choices, and other human dimensions usually deal only with broad categories of land use and land cover. Despite these important limitations, it is useful to review what we do know about the human dimensions of early successional landscapes in order to draw conclusions about their relevance to and role in wildlife habitat management and research. My objectives here are to: 1) characterize the key human dimensions of forest landscapes, 2) identify actual and probable relationships between people and early successional landscapes in the eastern U.S., and 3) discuss implications of managing early successional landscapes for wildlife and people.

[P]eople's recreational backgrounds can affect how they aesthetically perceive early successional landscapes and the ways in which those landscapes are managed.

The human dimensions of forest landscapes

The ways in which people relate to and interact with forest landscapes are as varied and diverse as the landscapes themselves. Some key categories of human interactions are: timber and nontimber forest products, visual and aesthetic perceptions, and recreational uses and choices. For each category I briefly summarize some of the major findings from existing research, then apply this knowledge to selected types and structural characteristics of early successional landscapes in the eastern U.S.

Timber and nontimber forest products

Statistics compiled for the 1992 Resources Planning Act (RPA) national assessment of forest resources show that 94% (144.5 million ha) of forest land cover in the eastern U.S. is classified as timberland that is potentially available for harvesting (Powell et al. 1994). Where timber production is an important goal, forest managers tend to favor a greater proportion of early successional tree species than might occur naturally. For example, aspen–birch (e.g., *Populus tremuloides, Betula papyrifera*)-dominated forests currently account for 16% of all timberlands in the north-central region, whereas in pre-European settlement times their occurrence was uncommon (Kotar 1997). Along with preferences for early successional species types, timber harvesting along with other human and natural disturbances keeps about 23% of all eastern U.S. timberlands in an early successional, seedling–sapling stage (Powell et al. 1994), though this percentage can vary greatly with location within the region (see Trani et al. 2001).

The contribution of timber resources to the economy of the eastern U.S. also varies considerably within the region. In the Northeast, only about 6% of the workforce is engaged in forest-related industries, whereas in the Southeast it is more than double that (Haynes 1990). Despite these differences, all of the eastern U.S. depends on important early successional species such as aspen (*Populus tremuloides* and *Populus grandidentata*) and southern pine (e.g., *Pinus palustris, Pinus echninata)* to provide significant portions of raw material upon which the region's timber industries depend. In the eastern U.S., early successional species are particularly important to high-value forest industries such as pulp and paper manufacturing. These industries, prominent in the northern and southern parts of the region, generally pay the highest wages of all timber-related industries and in 1982 employed nearly 200,000 individuals and generated shipments valued at more than $28 billion (Haynes 1990).

In addition to the timber resource, there is an increasing awareness of the importance of nontimber forest products and the need to manage forests to provide these products for commercial, subsistence, recreation, and other purposes. Nontimber forest products (NTFPs) generally include all wildlife and nontimber vegetation in forest and other natural landscapes and can be used for food, wildcraft, medicinal, cosmetic, religious, and other purposes. A multiyear national assessment of NTFPs in the U.S. is

Early successional landscapes provide diverse wildlife-related recreational opportunities, such as birding, that appeal to a wide range of people.

Table 1. Examples of early successional nontimber forest products found in the Upper Peninsula of Michigan, USA (adapted from Emery 1998).

	Functional uses				Livelihood uses			
Common name	M	C	E	F	PC	BG	SR	SP[a]
balsam, boughs				X	X		X	X
balsam, cones				X			X	
balsam, needles	X				X	X		
balsam, pitch	X				X			
berries, blackberry			X		X	X	X	X
berries, blueberry			X		X	X	X	X
berries, raspberry			X		X	X	X	X
berries, thimbleberry			X		X		X	X
birch, bark	X	X		X	X	X		X
birch, root				X				
birch, sections				X				X
birch, twigs		X		X			X	X
sweet fern		X	X	X	X	X		
sweet grass		X		X	X	X		X
wild rose hips			X	X				X
wild rose petals	X				X			
willow, twigs				X	X	X		X

[a] M = medicinal, C = ceremonial–cultural, E = edibles, F = floral–nursery–craft, PC = personal consumption, BG = barter–gift, SR = sale raw form, SP = sale processed form

almost complete (Jones et al., in press), and regional and local studies have highlighted the importance of early successional forests in providing a significant portion of these products. For example, research by Emery (1998) in the Upper Peninsula of Michigan documented that 138 products from more than 80 species of plants played important roles in the livelihoods of the households studied. Early successional species identified by Emery (1998) include trees such as birch (*Betula papyrifera* and *Betula nigra*; bark, twigs, roots) and balsam fir (*Abies balsamea*, boughs and cones) used in various wildcrafts, shrubs with edible berries (e.g., blueberry [*Vaccinium angustifolium*], blackberry [*Rubus fruticosus*]), and ground-cover plants such as sweet fern (*Comptonia peregrina*), and sweet grass (*Hierochloe odorata*) that have cultural and ceremonial uses (Table 1).

Given the importance of early successional species to the timber and NTFP communities of the eastern U.S., there are important reasons to consider efforts to maintain or increase their extent and availability. But with only 16% of timberlands held by private industry (Powell et al. 1994) and likely much less held by NTFP gatherers, this is an increasingly difficult task. Moreover, public lands, accounting for 14% of all eastern U.S. timberlands, are increasingly being managed to provide a more diverse array of benefits and values that the public demands. This includes management for recreation and aesthetics (to be discussed in more detail later) that often favors a more mature forest condition as opposed to early successional stages. The same trend may be occurring with nonindustrial private forestlands, which account for 70% of eastern U.S. timberlands. In many parts of the region, these lands are being subdivided and sold as smaller forest parcels and there are concerns that the new owners may be less concerned about timber values of the land than aesthetic and recreational ones (Gobster et al. 2000).

A major consequence of the trends described above, along with other factors, is that the land area of important early successional forest types is declining in the eastern U.S. This includes a 31% decrease in the area of aspen–birch, a 15% decrease in loblolly–shortleaf pine (*Pinus taeda* and *Pinus echinata*), and a 46% decrease in the area of longleaf–slash pine (*Pinus palustris* and *Pinus elliotti*) timberlands between 1963 and 1992. Along with changing forest types, the timberlands of the eastern U.S. are getting older, especially in the northern half of the region. There, the area of sawtimber has increased by 53% between 1963 and 1992, whereas the area in seedlings or saplings has decreased by 22% (Flather et al. 1999, see also Trani et al. 2001).

Visual and aesthetic perceptions

Sight is by far the most important sensory perception of humans, and thus the appearance of a landscape plays a major role in how it is appreciated and used by people (e.g., Bell 2000). Various theories of landscape preference have been developed and applied to forest and other natural environments over the last 3 decades, and they have implications for how different types or structures of early successional landscapes might be evaluated by people. Bioevolutionary theories of Appleton (1984) and others maintain that our preferences are at least in part geared genetically to favor landscapes that provide a prospect and a refuge—that is, allow people to see without being seen. Informational theories of Kaplan and Kaplan (1989) and others coincide with bioevolutionary theory, adding that humans prefer some degree of complexity and mystery in the landscape, but not so much that these landscapes lack coherence and legibility. In other words, we like landscapes that pique our interest and invite exploration, but we also need to be able to understand those landscapes so we can avoid danger or the risk of getting lost.

Oak-savanna landscapes of the eastern U.S. are good examples of early successional landscapes that might be preferred in the context of these theories. Reminiscent of our species' origin on the African savanna, these landscapes are high in prospect and refuge; they have a smooth ground plane that provides mobility, an open landscapes are managed. We also can look more directly at how early successional landscapes are used for recreation by examining the activities recreationists engage in and the environments in which those activities occur. The disciplines of human ecology, environmental psychology, leisure studies, and recreational geography have all examined people's outdoor recreational behavior as a function of their environmental context. The Forest Service's (1982) Recreation Opportunity Spectrum system for planning and managing outdoor recreation in the national forests is premised on the idea that people seek environments and activities that provide the kinds of personal and social benefits they desire. Additionally, Field et al. (1985), Greer (1990), and others have used the concept of "recreation habitats" to identify and study the attributes of sites that facilitate particular recreation activities.

Within this context, researchers have studied the landscape preferences and choices of different forest recreation users and have found that early successional landscapes play a varied role in terms of their importance. For example, campers tend to prefer more mature forests over early successional ones; they prefer shady sites to those that are more open and do not rate the screening that might be afforded by early successional vegetation as being as important as other characteristics such as flat ground or proximity to a water body (Bumgardner et al. 1988, Brunson and Shelby 1990). Trail users, on the other hand, tend to prefer a more heterogeneous landscape that might include some early successional landscapes and early successional stages of forest along with more mature forest conditions (e.g., Axelsson-Lindgren and Sorte 1987).

Wildlife-related recreation perhaps bears the closest correspondence to the type and structural characteristics of forest landscapes of all recreational activities; wildlife-oriented recreation is often where recreation habitat is synonymous with wildlife habitat. Hunters, wildlife photographers, birders, and other wildlife-oriented recreationists derive a great deal of satisfaction by "bagging" their prey (Bryan 1979), and whether that means a kill, a photograph, or a checkmark on a life list, those engaged in wildlife-oriented recreation are quick to learn the importance of being in or near the right habitat. These habitat–wildlife relationships are learned through experience, passed on from expert to novice, or studied with the help of field guides and other materials. Habitat-oriented wildlife guides can be invaluable in this respect. For example, Benyus's (1989) *Northwoods Wildlife: A Watcher's Guide to Habitats* begins with a habitat key and describes the constellation of plants and animals one is likely to find in 18 different habitat types in northern Minnesota, Wisconsin, and Michigan. Early successional habitat types form an important part of the book and include several kinds of forested and nonforested habitats such as small openings and edges, large fields, and young broadleaf upland forests.

Habitat types and wildlife species can be used as indicators to gauge the importance of early successional landscapes for wildlife-oriented recreation, and the United States Fish and Wildlife Service and United States Bureau of Census's *National Survey of Fishing, Hunting, and Wildlife-associated Recreation* provides statistics on activity participation using habitat and species groupings. The most recently available data are from surveys conducted in 1995–1996, and previous surveys (conducted every 5 years since 1955) can be used to help understand trends in participation. Statistics for 1996 show that 7% of the U.S. population aged 16 and older, nearly 14 million Americans, hunted in the previous 4 months, whereas 16% or 23.7 million watched wildlife away from home. Trend data (Figure 1) for 1980–1995 for the U.S.

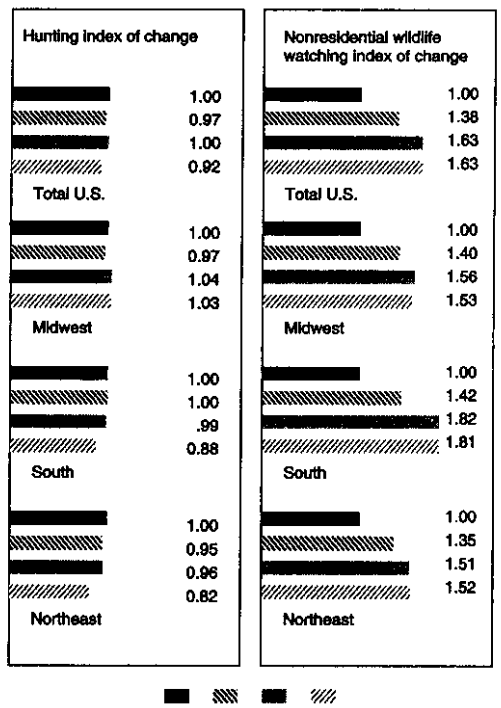

Figure 1. Index of change (1980 base year = 1.00) in percentage of U.S. residents 6 years and older participating in selected wildlife-related recreation activities 1980–1995 for total U.S. and eastern U.S. subregions (adapted from Aiken 1999).

Table 2. Participation in early successional wildlife-related recreation, U.S. population age 16 and older, 1980–1996.

	Hunting				Nonresidential wildlife watching			
Year	Deer	Grouse	All Hunting	% U.S. pop.	Brush	Open field	All sites	% U.S. pop.
1980	11,400,000	2,309,000	17,444,000	10	12,710,000	12,595,000	28,822,000	17
1985	11,987,000	2,190,000	16,684,000	9	10,355,000	11,384,000	29,347,000	16
1991	10,277,000	1,375,000	14,063,000	7	16,791,000	16,240,000	29,999,000	16
1996	10,722,000	1,220,000	13,975,000	7	14,065,000	14,849,000	23,652,000	12

Sources: United States Fish and Wildlife Service and United States Census Bureau (1982, 1988, 1993, 1997).

show that hunting in general is dropping in popularity, whereas nonresidential (away from home) wildlife watching is increasing (Aiken 1999). The greatest regional drop in participation was for hunting in the Northeast, which experienced an 18% decrease in the number of residents ages 6 years and up who hunted, whereas the greatest rise in participation was for nonresidential wildlife watching in the South, which saw an 81% increase from 1980 to 1995.

Statistics for species and habitat type are not published at the regional level, but nationwide data I compiled from the individual pentennial surveys give a reasonable picture of the importance of early successional communities (United States Fish and Wildlife Service and United States Bureau of Census 1982, 1988, 1993, 1997; Table 2). Deer (*Odocoileus* spp.) and grouse–prairie chicken (e.g., *Bonasa umbellus*, *Tympanuchus* spp.) are 2 species categories that depend on early successional communities. Deer hunting is by far the most popular type of hunting, engaged in by 77% of all hunters (16+ yrs) in 1996; by contrast, grouse–prairie-chicken hunting was confined to only about 9% of hunters. Both activities saw a drop in participation during 1980–1996, with deer hunting decreasing by 6% and grouse–prairie-chicken by nearly half (48%). For nonresidential wildlife watching, brush areas and open fields are 2 types of sites identified in the survey that are clearly early successional in nature. Both types were visited by more than 60% of nonresidential wildlife watchers aged 16 years and older in 1996. Visitation to these 2 types of sites has risen from 1980 to 1996 by more than 8%, though it is down from highs in 1991.

Implications

Information compiled on timber and nontimber forest products, visual and aesthetic perceptions, and recreational uses and choices all show that early successional landscapes play important roles in people's lives. It is impossible to calculate, however, whether this means there should be more or less in the way of early successional landscapes in the eastern U.S. than is currently present. Grouse hunters, for example, may desire mature trees so that they may hear owls, and those who weave baskets from willow (*Salix* spp.) shrubs found at the forest edge may use those baskets to collect mushrooms found deeper in the forest. Instead of arguing whose interests should be better served, forest managers and stakeholders should work together to help ensure that the forests of the eastern U.S. provide a spectrum of opportunities and experiences for people that in turn encompass a spectrum of early successional and other landscape and habitat types. What follows are some general recommendations for forest planning and design, communications to stakeholder groups, and research directions for advancing our understanding of the human dimensions of early successional landscapes with respect to wildlife and wildlife habitat.

Forest planning and design

Early successional landscapes supply important products to people, not only in terms of timber but increasingly for a variety of nontimber forest products used for commercial, subsistence, and cultural purposes. We are only beginning to realize the diversity of these products and how we might better provide them. As our knowledge of NTFPs increases with work such as the national assessment mentioned earlier, such information should be integrated into forest planning and design efforts to provide for these uses along with wildlife and other benefits and uses.

Early successional landscapes also supply important aesthetic and recreational benefits to people. Forest planners and landscape architects should look closely at the characteristics of early successional landscapes to understand the spectrum of recreation habitats they provide for site- and regional-scale planning and design. Using site-scale design guidelines by Ryan (2000) and others, forest landscape architects may be able to make some early successional landscapes more visually interesting and comfortable for people, yet still maintain the importance and integrity of those landscapes for the wildlife and plant species that depend on them. This might include such things as planting some showy native plants along trails in a visually homogeneous area to provide aesthetic diversity, planting native food-producing plants for wildlife near observation points to increase the chances for people to see wildlife, and locating trails in large, open ecosystems such as prairies near available canopy trees to provide occasional shade for people during their outings.

At the regional scale, design and planning systems for recreation and aesthetics also might be improved with better integration of information on ecology and wildlife habitat requirements. For the United States Forest Service, the primary developer of such systems in the U.S., some of this has happened in recent years since revision of its principal system for landscape aesthetics, the Scenery Management System or SMS (United States Forest Service 1995). SMS is built on a foundation of ecosystem management and uses ecological factors to describe key aspects of aesthetic quality. The Forest Service's companion system for recreation, the Recreation Opportunity System (United States Forest Service 1982), could benefit from a similar type of ecosystem integration. For early successional wildlife in particular, more detailed information about visual and recreational considerations could be provided with a handbook dedicated to landscape design and planning for wildlife. Similar detailed handbooks exist for timber, fire, utilities, and other topics, but the *Wildlife Habitat Management* handbook, which has existed in draft form since the mid-1980s, has yet to be published. As these topical handbooks are revised to conform to the Scenery Management System, publication of a wildlife handbook should be reconsidered.

Communications

Along with planning and design, communication with forest stakeholders can go far to describe benefits of early successional landscapes for wildlife and related concerns. Elsewhere (e.g., Gobster 1999) I have described how the idea of an "ecological aesthetic" might help to expand people's appreciation for some types of landscapes, such as prairies, which are not thought of as scenic in the conventional sense. Communication plays an important role in cultivating this more ecologically oriented appreciation for landscapes. For example, information can be a key tool in conveying knowledge about the intent and purpose behind early successional landscapes, especially for some management activities such as prescribed burning, where it is difficult to use design to increase public acceptance of the activity. On-site information such as signs, interpretive nature trails, stewardship programs, and the like can help communicate messages to the public. Habitat guides and brochures can be particularly useful for off-site communication.

Site design, such as trails and right-of-way mowing, and on-site information, such as signage, can often enhance the recreational and aesthetic benefits of early successional landscapes for people, especially in urban settings.

Along with such communications, on-the-ground experience and involvement can go far in helping people better understand and appreciate early successional landscapes. This experience can be gained in many ways, such as through self-guided nature tours and nature-oriented recreation such as birding, plant identification, hunting, and nature photography. Directed activities, such as participation in ecosystem restoration, are particularly valuable ways through which forest users can gain experience and appreciation of early successional systems and processes. This type of participation is less easy to accomplish on a large scale but can be extremely effective on a smaller, single-project basis. People who participate in such activities on a continuing basis often find that what began as an uncommon leisure activity has evolved into a relationship with the land that has deep aesthetic, symbolic, and spiritual implications.

Research needs

Finally, more social science research needs to be conducted to better understand the human dimensions of early successional landscapes. This includes studies that contribute to our knowledge about the benefits and uses of products from these landscapes, as well as a more refined understanding of how different kinds of landscapes and landscape management alternatives affect people's aesthetic perceptions and recreational uses. The need for further research is particularly true for nontimber-oriented studies, as there is little information on how people respond to different types of early successional landscapes as well as natural disturbances that create and maintain them (Gobster 1999). Early successional habitat could be built into these studies, for example, to gauge how the public perceives efforts to restore and manage landscapes for grassland birds. Research information related to wildlife-oriented recreation use such as hunting and wildlife watching also would be welcome, particularly by managers and groups concerned about the decline in hunting and hunting opportunities in the eastern U.S. (e.g., Flather et al. 1999).

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Conservation approaches for woody, early successional communities in the eastern United States

by Frank R. Thompson, III, and Richard M. DeGraaf

There is significant concern about the status of some early successional wildlife because of recent declines in populations and amount of habitat in the eastern United States (U.S.). We review types of semi-wooded, early successional habitats in the eastern U.S. and information on their status, and discuss management and planning approaches for their conservation. These habitats are dominated by persistent shrubs, seedling-sapling-sized trees, grasses, and forbs. The area of seedling-sapling forests and many natural shrubland habitats have declined in most of the eastern U.S. Silviculture creates early successional habitats primarily by regenerating stands. The selection of a regeneration method, size and distribution of cuts, and rotation age or reentry period influence availability of these habitats. Multi-scale planning approaches can be used to address regional concerns for these habitats and biological diversity, while facilitating landscape and local planning. We suggest that management for early successional communities is an important issue that should be addressed in conservation and land-management planning. Professional land managers and planners and the public need to address how many of these wildlife species we want and how we want them distributed throughout the region. In many landscapes silviculture will play an important role in providing habitat for these species.

Key Words early successional wildlife, historic range of variability, land-management planning, multi-scale, seedling-sapling, shrublands, silviculture

Perhaps for the first time since European settlement of North America, there is significant general concern for the status of at least some early successional wildlife species and for early successional communities in general (Litvaitis 1993, Askins 1998). However, this concern is controversial. Managing successional habitat reduces habitat for late successional wildlife and communities. Early successional wildlife species are often considered to be "weedy" species that flourish at edges and require no specific management actions, especially in human-dominated landscapes. Numerous early successional species, however, are extinct, endangered or threatened, or considered sensitive species or species of management concern, largely because of habitat loss (see other papers in this special section on the status of various early successional wildlife species [Hunter et al. 2001, Livaitis

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2001, Dessecker and McAuley 2001] and forests [Trani et al. 2001]).

We review types of semi-wooded, early successional habitat in the eastern U.S. and some information on their status, especially those not covered by forest inventory data. Our focus is on habitats dominated by persistent shrubs, seedling–sapling-sized trees, grasses and forbs, and sometimes scattered mature trees. We review silvicultural methods for providing these habitats and briefly review management options for other woody, early successional habitats. We then present some approaches to address these habitats in land-management planning by discussing benchmarks for ecosystem conservation and multi-scale planning approaches.

Conservation and land-management planning should acknowledge that important ecological processes occur at multiple spatial scales.

Woody, early successional communities

Woody, early successional communities are dominated by shrubs, young trees, and to varying degree by grasses and forbs. In the eastern U.S., nearly all shrubby communities are successional. The most stable tend to be on very hydric sites (shrub wetlands) or very xeric sites or sites with shallow soils (barrens and glades). Succession is most rapid on established forest sites where tree reproduction grows rapidly following a severe canopy disturbance. Woody, early successional communities generally occur because of land abandonment and succession or disturbance and succession. Land abandoned by humans or beavers (*Castor canadensis*) is recolonized by grasses, forbs, shrubs, and trees. Forests regenerate after significant canopy loss from timber harvest, fire, wind, disease, or insects. Savannas, glades, barrens, and other xeric shrublands are maintained in an arrested state of succession by frequent fire or poor (e.g., dry, sandy, or shallow) soils.

There is concern for all these types of early successional communities. Trani et al. (2001) used forest inventory data to show that throughout the eastern U.S., except for the southern region, young forest habitats are declining in area. This is because of forest maturation resulting from reduced timber removals in proportion to forest growth and cessation of land abandonment and succession to old fields and young forest. Abandonment of open land probably reached a peak in New England in the late 1800s to mid-1900s (Litvaitis 1993, Trani et al. 2001), and a wave of early successional habitats followed. Today, the extent of early successional habitats in much of New England may have reverted to pre-Columbian conditions (Litvaitis et al. 1999).

There also is concern for the loss of other types of natural shrubland communities. Noss et al. (1995) assessed the status of ecosystems in the U.S. by using numerous sources to determine the extent ecosystems had been reduced in area or degraded. They identified 41 ecosystems that have declined by more than 98% and classified these as critically endangered. Fifty-five percent of these were grassland, savanna, or barrens communities; 24% were shrublands, 17% forests, 2% forested wetlands, and 2% aquatic. Within the eastern U.S. some specific examples of declines are 99.98% loss of oak (*Quercus* spp.) savanna in the Midwest, 99% loss of original oak barrens in Michigan, 100% loss of intact bluegrass (*Poa* spp.) savanna–woodland in Kentucky, 90% loss of limestone cedar (*Juniperus virginiana*) glades in Tennessee, and 90% of coastal heathland in southern New England (reviewed in Noss et al. 1995). Many of these losses are due to fire suppression and land development.

Silviculture and early successional habitats

Timber removals in eastern forests significantly affect the amount of woody, early successional habitat (Trani et al. 2001). Silviculture creates early successional habitats primarily by regeneration cuts, which remove existing trees to create environments favorable for tree reproduction (Smith et al. 1997). Silvicultural prescriptions can be developed for objectives ranging from wood production, to wildlife, to aesthetics. The specific landscape composition and pattern and type and amount of early successional habitat depend on the silvicultural system, time between regeneration cuts, size of regeneration cuts, and rotation age or reentry period.

Regeneration habitats compared to other woody, early successional habitats

Early successional habitats created by timber harvest are dominated by tree reproduction and differ from other woody, early successional habitats, but nevertheless provide habitat for many of the same species. For example, 3- to 5-year-old clear-cuts and cedar glades in the Missouri Ozarks have similar densities of some early successional birds (Table 1; A. Fink and F. Thompson, unpublished data). There are differences, however, in vegetation structure and disturbance regimes. Succession

Table 1. Mean ± SE of some characteristics of 3- to 5-year-old clear-cut and cedar glade habitats in the Missouri Ozarks.

Characteristic	3- to 5-year-old clear-cut	Cedar glade
Prairie warbler[a]	0.88 ± 0.16	0.76 ± 0.16
Yellow-breasted chat[a]	0.65 ± 0.17	0.45 ± 0.17
Blue-winged warbler[a]	0.39 ± 0.02	0.41 ± 0.02
Stems 1–3 cm dbh/ha	107 ± 11.1	27 ± 10.4
Stems 3–10 cm dbh/ha	5 ± 1.1	5 ± 1.0
% canopy cover	28 ± 3.0	32 ± 2.8
% ground cover grass	8 ± 3.4	24 ± 3.2
% ground cover forbs	8 ± 3.2	16 ± 2.9

[a] Territories/ha.

is arrested on glades due to frequent fire and shallow soils. Glades on average have more grasses and forbs but fewer woody stems than clear-cuts (Table 1, Figure 1), which also may be true for other natural shrubland habitats. Some shrubland habitats often have more vines and shrubs than do regeneration habitats and therefore may have some unique wildlife species (Askins 2001).

Regeneration habitats are often more ephemeral than other woody, early successional habitats. The growth of a forest stand after a major disturbance is characterized by 4 developmental stages: stand initiation, stem exclusion, understory reinitiation, and old growth (Oliver and Larson 1996). Major disturbances kill most large trees but may not destroy forest-floor herbs, shrubs, advanced regeneration, seed banks, and roots; all respond rapidly to the increased availability of light and nutrients. This period of stand initiation has great plant and animal diversity because of the mix of grasses, herbs, shrubs, and trees. The stand-initiation stage continues as long as the canopy remains open enough for seedlings to become established and to support ground vegetation.

The stem-exclusion stage begins when the canopy closes and increases in height and the growing space is occupied fully by trees. This stage is the end of early successional habitat for many wildlife species because the ground vegetation is shaded out and browse, herbage, and soft mast from shrubs are lost. Others species such as ruffed grouse (*Bonasa umbellus*) and American woodcock (*Scolopax minor*) prefer this stage because it provides dense overhead cover from young trees and lack of dense ground cover (Dessecker and McAuley 2001). Aspen (*Populus* spp.), birch (*Betula* spp.), and northern hardwood forests may remain in the stand-initiation stage for <10 years; midwestern oak stands may take >15 years to outgrow this stage (Figure 2).

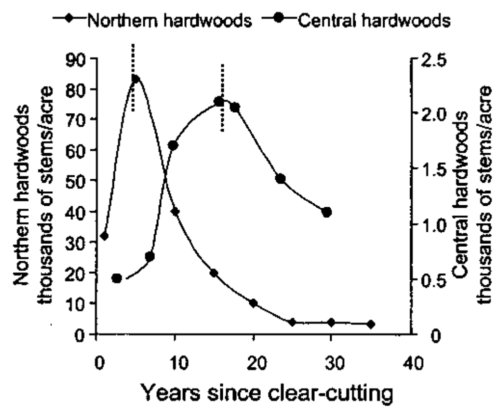

Figure 2. Patterns in tree-stem densities during stand development in northern hardwoods and central hardwoods during the stand-initiation stage (left of dotted line) and stem-exclusion stage (right of dotted line). Stem densities are not directly comparable between forest types due to differences in methods (adapted from Marquis 1967; Oliver and Larson 1996; Leak and Smith 1997; P. Johnson, United States Department of Agriculture, Forest Service, personal communication).

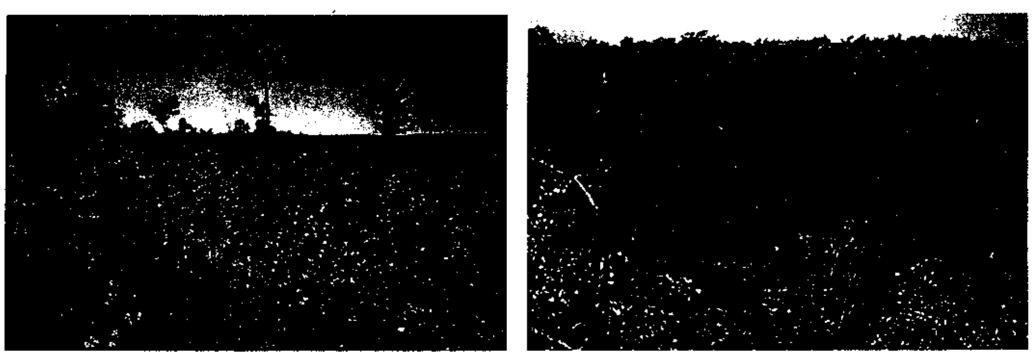

Figure 1. A 4-year-old oak forest regenerated by the clear-cut method (left) and a cedar glade (right) in the Missouri Ozarks.

Table 2. Number of years after clear-cutting eastern deciduous forest that breeding, early successional birds first appear, become common, and then decline. We assumed that some residual stems (snags and live trees) remain (DeGraaf 1987, Thompson et al. 1992, Thompson et al. 1996).

Bird Species	First appear	Become common	Decline
Ruffed grouse (drumming males)	10	15	20
Northern flicker	1	1	7–10
Olive-sided flycatcher (*Contopus cooperi*)	1	1	3–4
Willow flycatcher	1	2	5–7
Tree swallow (*Tachycineta bicolor*)	1	1	7–10
Winter wren	1	4	7–10
Eastern bluebird	1	1	2
Veery (*Catharus fuscescens*)	3	10	20
Swainson's thrush	2	4	15
Cedar waxwing	2	4	7–10
Blue-winged warbler	1	2	7–10
Chestnut-sided warbler	2	4	10
Prairie warbler	2	2	10
Black-and-white warbler (*Mniotilta varia*)	3	10	a
Mourning warbler	2	5	10
Common yellowthroat	2	6	10
Canada warbler (*Wilsonia canadensis*)	5	15	a
Yellow-breasted chat	2	2	7–10
Field sparrow	1	2	5
White-throated sparrow	1	2	a
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	3	15	a
Indigo bunting	1	2	7–10
American goldfinch	2	6	7–10

[a] Present until next cutting cycle.

The length of time a forest provides habitat for early successional species also is dependent on site quality. Site index is the height that dominant trees are expected to reach in a fixed period and is a measure of site quality. Sites with lower site index will therefore remain in an early successional stage longer. For example, a 20-year-old aspen stand with a site index of 80 has 3,681 trees/ha and is 13.4 m tall, on average. In contrast, a 20-year-old stand with a site index of 40 will have 10,130 trees/ha and is only 6.7 m tall (Brown and Gevorkiantz 1934, Perola 1977).

Because of rapid succession, breeding bird composition changes quite rapidly in the first 10 to 15 years after complete clear-cutting. Many of the earliest arriving birds decline in just a few years as habitat conditions change (Table 2). In the White Mountains of New Hampshire, regenerating stands 1 to 5 years old contain about 28 bird species. Of these, 5 are restricted to that stage. Sapling stands contain about 30 species and pole-timber stands only about half as many (DeGraaf 1987). White-throated sparrows (*Zonotrichia albicollis*), winter wrens (*Troglodytes troglodytes*), and willow flycatchers (*Empidonax traillii*) are generally abundant in the first growing season after complete removal of all live stems. Winter wrens are associated with dense slash and willow flycatchers with brushy habitats. If stubs with old woodpecker holes are left, eastern bluebirds (*Sialia sialis*) also are commonly present. Two years after clear-cutting, the number of species doubles; common yellowthroats (*Geothlypis trichas*), chestnut-sided warblers (*Dendroica pensylvanica*), cedar waxwings (*Bombycilla cedrorum*), American goldfinches (*Carduelis tristis*), and mourning warblers (*Oporornis philadelphia*) commonly invade, along with Swainson's thrushes (*Catharus ustulatus*), Eastern towhees (*Pipilo erythrophthalmus*), and American redstarts (*Setophaga ruticilla*). Northern flickers (*Colaptes auratus*) and white-throated sparrows remain present, but eastern bluebirds and sometimes winter wrens are gone. In the third growing season after clear-cutting, bird species numbers again double, with about a dozen new species added, mostly in low numbers. During the next 12 years, bird species composition changes substantially, but number of species usually does not change appreciably. In midwestern oak forests, yellow-breasted chats (*Icteria virens*), blue-winged warblers (*Vermivora pinus*), indigo buntings (*Passerina cyanea*), and field sparrows (*Spizella pusilla*) also become abundant after about 2 years (Thompson et al. 1996).

Old-field succession following land abandonment is a result of woody species invading from the surrounding landscape, and it can take much longer for a site to be reoccupied by trees than for a regenerating forest stand. Midwestern cedar glades succeed slowly to cedars and hardwoods because of fire and shallow soils and can support early successional wildlife for >30 years with no additional disturbance (Chambers 1994).

Silvicultural methods

The selection of even- or uneven-aged silvicultural systems is an important consideration for early successional wildlife. Uneven-aged or selection systems regenerate forest in patches created by removing single or small groups of trees while even-aged systems regenerate trees in large patches that can range from 0.5 to 20 ha or more. Single-tree selection results in the least canopy disturbance and may not allow enough light to reach the forest floor to support light-demanding plants. This results in limited and dispersed tree reproduction, shrubs, and herbaceous plants (E. F. Loewenstein, personal communication), which may not provide sufficient structure

Table 3. Numbers of stems (2- to 25-mm diameter, in thousands of stems per hectare) by species, residual basal area, and treatment; an example from New England northern hardwoods 9 years post-cutting (adapted from Leak and Solomon 1975).

Residual basal area (sq. ft.)	Treatment	Beech[a]	Yellow birch	Sugar maple	Red maple	Paper birch	White ash	Red spruce	Eastern hemlock	Balsam fir	Pin cherry	Striped maple	Rubus	Yew	Hobble-bush	Other	Total
100	Uncut–very lightly cut	27.4	2.3	2.5	17.2	1.1	2.6	0.0	0.3	0.1	3.1	4.2	0.6	6.5	21.0	1.0	89.9
80	Single tree selection	38.3	8.7	4.9	14.4	2.1	5.7	0.1	0.7	0.0	3.5	9.8	2.4	1.0	23.6	0.2	115.6
60	High density shelterwood	50.9	9.6	5.3	18.2	1.7	7.9	0.0	1.3	0.3	3.4	7.4	1.2	18.2	19.2	1.4	146.1
40	Low density shelterwood	36.9	5.3	3.6	62.9	4.6	8.4	0.1	1.0	0.0	6.8	14.1	3.0	37.7	34.9	0.9	220.3
0[a]	Patch clearcut	14.8	24.0	17.5	11.1	42.0	4.4	58.1	5.4	100.3	35.1	313.2					

[a] Beech, *Fagus grandifolia*; yellow birch, *Betula alleghaniensis*; sugar maple, *Acer saccharum*; red maple, *A. rubrum*; paper birch, *B. papyrifera*; white ash, *Fraxinus americana*; red spruce, *Picea rubens*; Eastern hemlock, *Tsuga canadensis*; balsam fir, *Abies balsamea*; pin cherry, *Prunus pensylvanica*; striped maple, *A. pensylvanicum*; rubus, *Rubus* spp.; yew, *Taxus canadensis*; hobblebush, *Viburnum lantanoides*.

[b] Second-growth patches (Marquis 1965), 3-year regeneration, undisturbed seedbeds only.

or browse for some early successional species. The group-selection method and even-aged methods produce recognizable patches of early successional habitat. When groups become large enough to allow full sun to reach the forest floor, they essentially are small clear-cuts. The group-selection method and even-aged methods can produce similar amounts of habitat at a landscape scale, but the spatial distribution of habitats, patch size, and amount of edge in the landscape can be very different. Commercial timber rotations in natural stands under even-aged management are typically 40 to 100 years and regenerate 25% to 10% of the landscape/decade. Stands managed by selection methods (uneven-aged management) are entered typically every 10 to 20 years and some percentage of the stand is regenerated in single-tree or group openings.

Shifley et al. (2000) used a landscape model to simulate differences in the composition and structure of a midwestern oak forest under 5 management scenarios. All scenarios included wind and fire disturbances at recent historical levels. The resulting amounts of seedling- and sapling-sized forest varied somewhat predictably, based on the management scenario, and ranged from 10.9 % to 0.1% (Figure 3*A* and *E*, respectively), but the size and distribution of seedling and sapling forest patches varied greatly. Mean patch size of seedling and sapling forest was greater in scenarios *A* and *B* (1.7 ha) than scenarios *C* and *D* (0.3 and 0.2 ha, respectively; Figure 3). Patch size also affects the amount of edge between early successional and late successional forest. For comparable areas of regeneration, uneven-aged management results in more edge than even-aged management (Thompson 1993, Shifley et al. 2000).

The number of mature residual trees, either live or dead, in regeneration cuts affects vegetation structure and composition of a stand and wildlife use. Mature trees may be left in a shelterwood or seed-tree-regeneration cut to provide seed and modify the microclimate, or for

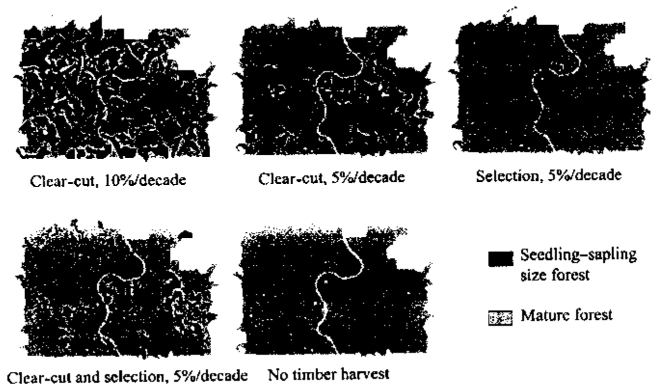

Figure 3. Simulated effects of forest management in a 3,200-ha central hardwood landscape for 5 management scenarios that differ by silvicultural method (clear-cut or group-selection method) and level of harvest (0, 5, or 10% /decade). The depicted patterns are the result of 100 years of simulated management (adapted from Shifley et al. 2000).

aesthetic or wildlife benefits. High levels of residual trees generally result in lesser densities of regenerating trees, especially of shade-intolerant trees, shrubs, grasses, and forbs (Table 3), which are important to many early successional wildlife species. Residual trees can increase wildlife diversity by providing additional structures, especially for cavity users.

For at least some wildlife species, size and distribution of habitat patches are probably equally important to the total amount of habitat. The selection of silvicultural methods and the resultant patch size and amount of edge affect early successional species differently. Many early successional species use a range of clear-cut sizes (Krementz and Christie 1999), including some <1 ha (Askins 1998), but prairie warblers (*Dendroica discolor*) and yellow-breasted chats do not use isolated, small-group-selection cuts (Annand and Thompson 1997). Once regeneration patches are large enough to be occupied, nest success may not vary. Nest success of some early successional songbirds does not differ among group-selection cuts and clear-cuts (King et al. 2001; R. L. Clawson, Missouri Department of Conservation, unpublished data). New England cottontails, however, may suffer greater mortality in smaller habitat patches (Barbour and Litvaitis 1993). Songbirds nesting in regeneration habitats have species-specific patterns of edge preference or avoidance and lesser or greater nest predation near edges (Woodward et al., in press).

We believe that in most landscapes availability of large patches will be more limiting than that of small patches and that even-aged silvicultural practices are most suitable where early successional wildlife is a priority. Even-aged management in New England northern hardwoods provides habitat for more breeding bird species than does uneven-aged management. A range of even-aged stands of northern hardwoods (seedling, sapling, pole timber, and sawtimber) contains more than twice as many bird species as do extensive uneven-aged stands. All species that occur in the uneven-aged stands also occur in one or more size-classes of even-aged stands. No breeding birds are restricted to uneven-aged conditions. However, many species are restricted to even-aged habitats, especially in regeneration and sapling stands, and so are present for only a brief period in the life of the stand (DeGraaf 1987).

Natural disturbance as a model for silviculture

Natural disturbance regimes may provide effective models to manage forests as renewable resources while retaining biological diversity (Attiwill 1994). For example, wildfire was the dominant disturbance agent in boreal forests and occurred in large stand-replacing fires. Presently fire control and clear-cutting have largely replaced wildfires, and the result is smaller, more uniformly distributed patches of young forest (Hunter 1993, Delong and Tanner 1996). Clear-cuts could be made much larger to mimic the full range of naturally occurring disturbances (≥5,000 ha), but it is unlikely that society would tolerate such large clear-cuts. Hunter (1993) presented alternatives including clustering moderately sized clear-cuts. Stand-replacing fires were less common in central hardwood forests and especially northern hardwoods, but occasional large fires did occur. Windthrow of a single tree or several trees was common, and occasional catastrophic wind (hurricanes and tornadoes) created large habitat patches (see reviews by Lorimer 2001; Dey, in press).

The application of any one silvicultural method with a narrow range of regeneration patch sizes will create a more uniform and narrow distribution of habitat patches than the natural disturbance regimes described above. One approach to increase spatial heterogeneity is to allocate equal land area to regeneration cut sizes, and if the total cut is equal in each area, the resulting patch-size distribution across the landscape will include many more small cuts than large (Hunter 1990) and resemble a reverse, J-shaped distribution. We illustrated this concept for an eastern forest on a 100-year rotation with group-selection cuts (0.1 ha) and a range of clear-cut sizes (1 to 100 ha, Figure 4).

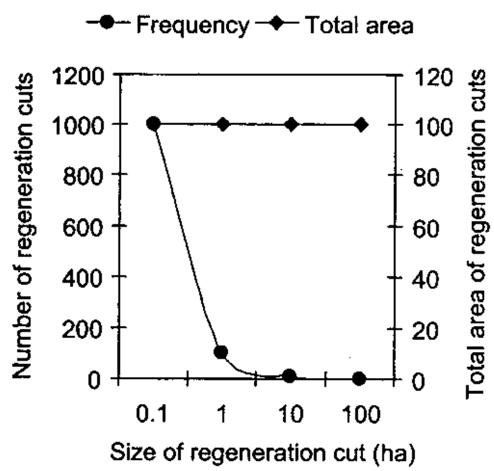

Figure 4. Hypothetical distribution of patch sizes of early successional habitat resulting from regenerating equal areas by the group-selection method and small, moderate, and large clear-cuts.

Management of shrubland habitats

Woody, early successional habitats, other than regeneration cuts, depend on a variety of natural disturbances. One approach to their management is to simply let natural disturbance (i.e., fire) occur. To sustain communities through time, such natural disturbance regimes would have to be permitted over large areas to account for their stochastic nature. However, given the highly developed nature of eastern landscapes and their fragmented ownership and land cover, this may be possible only on the largest wilderness areas. In much of the eastern forest, early successional species depend on managed or artificial habitats (Askins 1998).

A variety of management techniques exists to set back succession and reduce competition with desired vegetation. Management options include herbicides or mechanical methods such as chaining, cabling, scalping, tillage with disks or plows, or felling with chainsaws (Yoakum et al. 1980). Prescribed fire is a logical choice to restore and maintain fire-dependent communities. Fire can be used to manipulate both the woody and herbaceous composition of habitats and has the general effect of setting back woody encroachment in these habitats (Wright 1974, Bragg and Hulbert 1976, Lewis et al. 1981). Often, however, burning is constrained by limitations on funding or personnel, fragmented or small ownerships, and a limited number of suitable days each year for burning. In these circumstances the only alternatives may be mechanical or chemical treatments, but if expense or labor is an issue, these also will be impractical. Shrubland habitats can be managed to last longer by selectively removing trees and encouraging shrubs, grasses, and ferns to dominate. This can be achieved by selectively felling tall trees and applying herbicide to the stumps (see Askins 1998 for review). Management of shrublands by these techniques can be expensive and there is usually no financial incentive for private landowners. This contrasts with management of early successional forest by silvicultural techniques that produce income from the harvest of trees.

Land-management planning for early successional habitats

Putting concerns for early successional communities in perspective and balancing them with other conservation issues is a challenge for land managers and planners. It requires integrating our best ecological science with social perspectives and demands for resources. Legislative mandates such as the National Forest Management Act of 1976 require planners to consider the diversity of plant and animal communities and the distribution of individuals in the planning area. Nearly all plans identify some subset of species that are considered special and are treated as focal species for planning and management. Conflicts arise because of differences in habitat requirements among species; it is impossible to provide for some species on a fixed land base without impacting other species.

Ecosystem approaches are advocated to conserve biological diversity as a solution to some of the shortcomings of species-level approaches. Ecosystem- or community-level conservation approaches are referred to as a "coarse filter" approach because they can address the conservation needs of most species without conservation planning for individual species (Hunter 1990, Probst and Crow 1991, Noss et al. 1995). Species-level or "fine filter" approaches can be critical for endangered species or desired for other focal species; however, they can be extremely expensive and impractical for species for which we have inadequate knowledge and can greatly increase the complexity of multi-species or multiple-use planning.

Recently scientists have suggested that multi-scale approaches are necessary because some characteristics of sustainability are best viewed from a regional perspective while others are more appropriately considered at a landscape or site-specific scale (Probst and Crow 1991, Freemark et al. 1995, Committee of Scientists 1999). This approach often begins with a large-scale assessment that includes the distribution of major vegetation types and successional stages and some historical perspective of these distributions. We use selected examples to demonstrate the application of these approaches to the conservation of early successional habitats. We review some issues concerning the selection of appropriate benchmarks for the distribution of early successional communities and the application of hierarchical, multi-scale planning approaches.

Benchmarks for ecosystem management

One difficulty with ecosystem approaches is setting benchmarks for conservation. In a general sense, the goal of ecosystem conservation is to preserve a region's natural communities and biological diversity. In land planning and management, however, specific desired future conditions must be envisioned and described by landscape characteristics such as the aerial extent of ecosystems, habitat patch size, and habitat interspersion. The dominant approach for setting ecosystem goals has been to consider the historical distribution of ecosystems because it is assumed that conditions under which species persisted for long periods should indicate viable conditions for populations.

While the rationale to use historic conditions is logical, it may be difficult to select the appropriate historical period because natural and anthropogenic activities have not been stable in eastern North America since the last glaciation. After the Wisconsin glaciation, trees moved northward at different rates and did not occur in the communities we now recognize (see Davis 1981, for review). Askins (1998) speculated that prior to the occupation of North America by humans, gigantic browsing mammals created openings or open woodlands and savannas that provided habitat for early successional wildlife. About 10,000 years ago, humans inhabited eastern North America. Much of the East was subjected to slash-and-burn agriculture by Native Americans for at least the past 1,000 years. Beginning in the mid-1700s and culminating in the mid-1800s, much of New England was cleared for agriculture and then abandoned and reclaimed by forest in the early 1900s (see DeGraaf and Miller 1996, Lorimer 2001).

There is significant controversy over what historic periods should be used and what should be considered natural (for example, see editorial by Hunter 1996 and letters by Haila 1997, Comer 1997), because of this varied history. One possibility is the period just prior to the colonization of North America by Europeans during the last 400 years, presumably because of the magnitude and speed of landscape change that occurred after that period. As discussed, however, Native Americans had significant impacts on the landscape in eastern North America. Another difficulty with this approach is our inability to estimate landscape conditions during these periods, but this has been attempted from historical accounts (Whitney 1994, Askins 2000) and analysis of lake sediments (Delcourt 1979, Watts 1983, Patterson and Sassaman 1988).

One approach that helps reduce controversy over selection of an appropriate benchmark is to acknowledge that a range of historic conditions was likely suitable for species persistence. The historic range of variability (HRV) refers to the historic patterns in a resource that are assumed related to the natural range of variability concept—that is, the expected variability in ecological conditions caused by climate fluctuations and natural disturbance regimes. This approach similarly assumes that the more proposed conditions differ from the conditions during the HRV, the greater the expected risk to native species, their habitats, and their long-term ecological productivity (Committee of Scientists 1999). It also requires selection of a historic time period and consideration of what is natural, but because the approach acknowledges a range of conditions, it may be less controversial than a specific benchmark. We suggest that planners acknowledge the full range of conditions that species occupied (pre- and post-settlement) and let other social benefits or goals in the planning process identify more specific benchmarks. Society's desire for more or less early successional wildlife, old-growth forest, or forest products will direct management from one end of the HRV to the other.

Multi-scale conservation planning

Population viability is determined by an interaction between local habitat factors, the landscape context of habitats, and regional or continental context of habitat biogeography and population levels. We believe that successful conservation planning requires a multi-scale approach that begins with regional-scale assessment of status of communities and establishes conservation priorities and goals, then at a subregional and landscape level identifies opportunities to address regional goals and sets landscape objectives, and then selects management prescriptions at the habitat patch or stand level to meet landscape objectives and regional goals (Freemark et al. 1995, Thompson et al. 1996, and others). A hierarchical approach acknowledges that some characteristics of sustainability are best viewed from a regional perspective, whereas others are more appropriately considered at a landscape or site-specific scale (Committee of Scientists 1999). By addressing the larger scale context first and setting regional goals, conflicts can be reduced at site-specific scales.

Managers and planners are accustomed to working at site-specific scales because this is how silviculture and other management are typically applied. Here we review some issues and planning approaches for early successional habitats at 2 larger scales that may sometimes be overlooked, yet provide necessary context for local decisions.

Regional scale. Examples of a regional scale are New England, Middle Atlantic, Great Lakes, Central Plains, Coastal South, and Interior South used by Trani et al. (2001) to assess trends in forest habitats, or the northern hardwood forest and the midwestern oak and oak–pine forest regions used by Lorimer (2001) to assess natural disturbance regimes. Regional goals can include the desired amount of major vegetation or forest types and the size structure of forests. A prerequisite to establishing regional goals is some type of regional assessment of the current and historic extent of flora and fauna, and knowledge of disturbance regimes (i.e., Ozark–Ouachita Highlands Assessment [United States Department of Agriculture 1999] and the Southern Appalachian Assessment [Southern Appalachian Man and Biosphere 1996]).

Issues at the regional scale for woody, early successional habitats are regional declines in early seral forest types and shrubland ecosystems and declines in seedling–sapling-size class in forests. For example, aspen–birch forests have declined 31% in the north-central region (Flather et al. 1999), longleaf–slash pine forests have declined 45% in the South (Flather et al. 1999), and oak savannas have declined 99.9% in the Midwest (Noss et al. 1995). The New England, Middle Atlantic, Central Plains, and Great Lakes regions all show decline in amount of seedling–sapling forest (Trani et al. 2001). Current extent of seedling–sapling forest as a percentage of forestland ranges from 16% in the Northeast to 32% of the Coastal South. When expressed as a percentage of the total land area, seedling–sapling forest is 13, 8, 3, 11, 8, 12, and 9% of the New England, Middle Atlantic, Central Plains, Great Lakes, Interior South, Coastal South, and the entire eastern region, respectively. It is difficult to put recent declines and current levels of seedling–sapling forest in the context of an HRV. Lorimer (2001) estimated that 1–14% of the northern hardwood forest region was in young forest. Up to 65% of midwestern states was prairie and savanna (Lorimer 2001), but it's difficult to identify how much of this was shrubland–young-tree habitat versus grassland. Young-forest habitat reached a peak throughout the eastern forests in the late nineteenth and early twentieth centuries, composing as much as 60% of most states.

The general perspective gained from this information is that in most regions early successional habitats are declining from peaks in abundance earlier this century. In some regions such as New England, early successional habitats are likely below presettlement levels (Litvaitis 1993, 2001). In northern and midwestern forests, current size-class structure may not differ greatly from presettlement times; however, certain grassland–shrub–tree ecosystems such as savanna and barrens have declined to less than 1% of their presettlement distribution. In fact, in all regions there are examples of natural shrubland communities that have declined (Noss et al. 1995).

Regional patterns in habitat fragmentation also are an important issue. Early successional habitats tend to be fragmented because they are patches created by disturbance events. There is evidence, however, that the landscape context of these habitats is important to species viability. Nesting success of forest songbirds tends to be low in fragmented landscapes with low amounts of forest cover; this also applies to species such as Kentucky warbler (*Oporornis formosus*), indigo bunting, and northern cardinal (*Cardinalis cardinalis*) that often nest in patches of early successional habitat in older forest (Robinson et al. 1995). Landscapes fragmented by human-dominated activities such as agriculture and development may contain greater numbers of predators (Donovan et al. 1997, Dijak and Thompson 2000) and brown-headed cowbirds (*Molothrus ater*, Donovan et al. 1997, Thompson et al. 2000), which affect nesting success of early successional species and forest species. Predators and cowbirds do not seem to respond to silvicultural practices in the same way as fragmentation of forests by nonforest land uses.

Subregional to landscape scale. At this scale we refer to areas of thousands to millions of hectares, such as a national forest, a county, a watershed, etc. Planners and managers can assess the ecological capabilities of the land (based on ecological classification systems), the current distribution of ecosystems and species, and local knowledge of disturbance regimes. This should provide the background to set specific goals (in the form of a range of acceptable variability) for the distribution of ecosystems and species that acknowledge regional goals and the ecological capability of the landscape under consideration. This scale requires knowledge of local disturbance regimes, ecosystem patterns, and the needs of featured species. These goals should be more specific than at the regional level—for example, the amount of forest size classes by forest type, and the amount of fire-dependent communities such as oak-savanna and cedar glades—and require specifying silvicultural treatments, including regeneration methods and rotation ages or reentry periods. Within the defined range of acceptable variability, opportunities should exist to manage for featured species or other benefits.

Planners and managers should consider spatial and temporal patterns in early successional habitats at this scale. We have advocated a range of patch sizes and silvicultural methods to meet the habitat needs of early successional wildlife and to mimic patterns created by natural disturbances. However, not all landscapes need to provide all patch sizes or even all habitats; a key element of a multi-scale approach is that diversity should not be maximized at small scales. For example, large regeneration patches may be provided on industrial or public lands, selection methods applied on small, fragmented private lands, and a mix of practices on public forestland. In managed forests, clustering regeneration cuts will provide some large habitat patches for early successional wildlife. These areas, however, will provide large habitat patches for forest wildlife in 10 to 60 years. Other species that require habitat diversity or interspersion will require great within-landscape diversity. Where early successional wildlife is a concern, planners and managers need to address the ephemeral nature of these habitats to maintain appropriate levels in the landscapes. This could mean providing a shifting mosaic of regeneration cuts and managing more permanent natural shrubland habitats with fire and other techniques.

Management decisions at a site or stand level will be easier if the objectives at large scales are well defined. Once these are defined and site capabilities are known, management guides can be used, including silvicultural guides (e.g., Leak et al. 1987, Clark 1989), habitat-based guides (e.g., DeGraaf et al. 1992, Hamel 1992), and guides focused on early successional communities (Thompson and Dessecker 1997). Prescriptions are not as well developed for prescribed fire or management of natural shrublands (but see Askins 1998).

Conclusions

Conservation and land-management planning should acknowledge that important ecological processes occur at multiple spatial scales. Hierarchical, multi-scale planning may be a useful framework to plan for multiple, sometimes competing land uses. A top-down approach is needed to establish priorities or objectives at regional and subregional scales for species, ecosystems, and ecological processes (e.g., the role of fire and silviculture). It is hoped that site-specific planning can then proceed with less controversy because it will be based on opportunities to address larger-scale goals and local site capabilities. A strictly local or bottom-up perspective for comprehensive resource planning can lead to high local diversity but low ecosystem integrity and conflicting prescriptions for multiple resources or species. By placing local decisions in a regional context, land managers and planners can direct local planning to meet different but complementary objectives.

Given the increasing worldwide demand for wood, a growing gap between wood fiber consumption and production in the U.S., and conservation concerns for some early successional species and communities, we suggest that management for early successional communities is an important issue that should be addressed in conservation and land-management planning. This issue provides a unique opportunity to simultaneously address production of a commodity (wood) with conservation. A wide range of regional and landscape conditions exists that will sustain early successional species. For some species in some regions, there is evidence that we are close to or even outside the limits of this range. For other species whose viability is not necessarily threatened, declining numbers have simply raised concern by conservationists or the public. For species whose viability is threatened, the mandate is clear for most conservation agencies. For those species that are not immediately threatened, conservationists, wildlife managers, land-management planners, and user groups should still address how many of these species we want and how we want them distributed throughout the region.

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