# *The* HIGHLANDS

## Critical Resources, Treasured Landscapes

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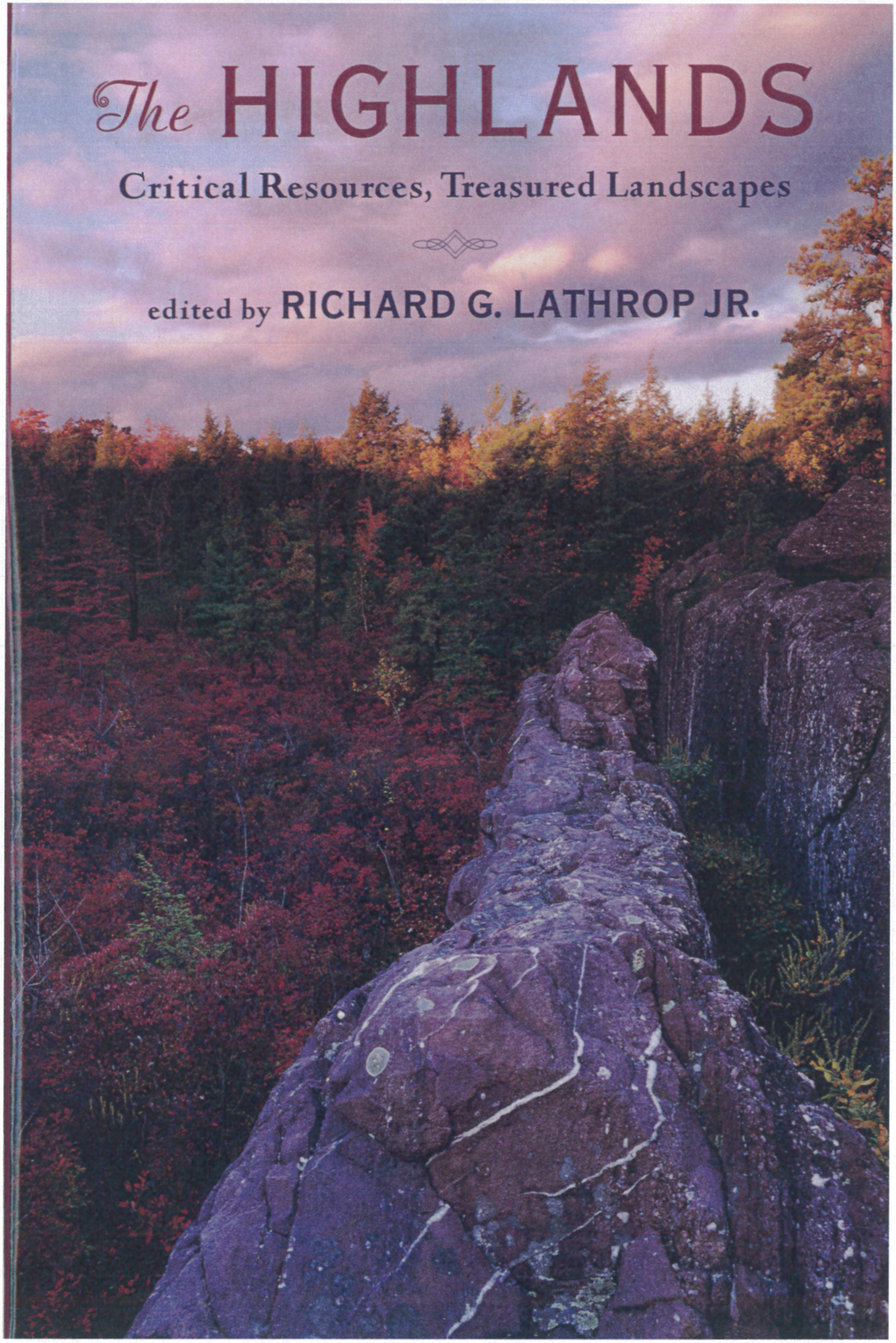

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# Forest Ecology

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## Introduction

Forests are earth's dominant vegetation type and are intimately intertwined with our lives. They produce much of the oxygen we breathe, supply much of the water we drink, provide material to build the houses in which we live, and are central to many facets of human endeavor. Forests function via processes and change over timescales that can be difficult for humans to appreciate. Failures to understand forest ecosystems have underlain some of the most momentous societal collapses in history (Diamond 2005). Forests of the Highlands are of direct importance to the lives of millions of people. But some of the changes now occurring in these forests may have unprecedented impacts on humans and other organisms around the region.

Forests are more than the sum of their parts. They are ecological systems interconnected by processes such as energy flow and nutrient cycling. Natural ecosystem functions provide many services and products of value to human societies. For example, we rely on forested watersheds as sources of high-quality drinking water because of their biogeochemical cycles, which filter many substances that we consider pollutants. For another example, photosynthesis by forests absorbs enormous amounts of atmospheric carbon dioxide each year, counteracting much of the carbon dioxide released by fossil fuel combustion and slowing the rate of anthropogenic climate change. Thus alteration of forest ecosystem processes can have far-reaching and enduring consequences.

Although forest cover in the Highlands region, as in much of eastern North America, is now more extensive than in the last 150 years, abundance does not necessarily imply good health. It is increasingly clear that, in some parts of the Highlands, forest function has been substantially altered and forest health has been compromised. We need to understand what services and products we need these forests for, and we must closely monitor their health so they can provide such needs for the foreseeable future.

In the remainder of this chapter I will describe current forests of the Highlands, evaluate aspects of their health, and review some of the changes that are occurring. I will focus on key areas of ecosystem health such as energy flow, biological diversity, nutrient cycling, and disturbance regimes. I will conclude by discussing future implications of these changes and some possible responses.



## Forests of the Highlands

The 250-mile-long (400+ km) Highlands province lies wholly within the "historic oak-chestnut forest" region (Braun 1967). Since the demise of the American chestnut (*Castanea dentata*), this regional forest type has often been termed "oak-hickory" despite the fact that hickories (*Carya* spp.) are only minor components of most stands. Oak trees (*Quercus* spp.) and their acorns, conversely, are iconic of the Highlands region and central to its ecology. Other abundant deciduous hardwoods in the region are red and sugar maple (*Acer rubrum* and *A. saccharum*), yellow poplar (*Liriodendron tulipifera*), hickories, birches (*Betula* spp.), ashes (*Fraxinus* spp.), and American beech (*Fagus grandifolia*). The most common conifers in the Highlands are eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), and pitch pine (*Pinus rigida*). Nonnative trees that may be locally abundant include Norway maple (*Acer platanoides*), Norway spruce (*Picea abies*), tree-of-heaven (*Ailanthus altissima*), European buckthorn (*Rhamnus cathartica*), and black locust (*Robinia pseudoacacia*). The Forest Service's Forest Inventory and Analysis (FIA) database indicates that the four most common local cover types in the Highlands are white oak/red oak/hickory; red oak; yellow poplar/white oak/red oak; and red maple/lowland hardwoods (Woudenberg et al. 2009; table 7.1).

The composition and structure of current Highlands forests reflect local climate, topography, and geologic substrate as well as the sequence of historical factors described in the previous chapter: heavy cutting and clearing, conversion of much forestland to pasture and other agricultural uses, widespread abandonment of these uses, and subsequent forest regrowth. Stone walls' characteristics attest to previous land uses, with ridges and steeper slopes most often having served as woodlots while gentler slopes and valleys were more often converted to pasture or cropland. The majority of the Highlands landscape was cultivated or developed at some time in the past, and forestlands that were not converted have nearly all been repeatedly cut, and many have burned. Canopy trees in these forests today either survived or in some cases thrived as a result of this heavy disturbance and in many woodlot areas also successfully contended with naturally low levels of soil nutrients. The frequent cutting cycles of the past favored hardwoods that readily regenerate from root sprouts such as red and chestnut oak (*Quercus rubra* and *Q. prinus*). The suppression of fires through much of the twentieth century also resulted in expansion of thin-barked species such as red maple. Nonnative organisms

*Table 7.1* **Characteristics of Forest Inventory and Analysis (FIA) Plots around the Highlands Region (2003–2008 data)**

| Region | % Forested plots | Stand age (yrs) | Basal area (ft²/ac) | Wood volume* | Above-ground biomass** | Tree height (ft) | Site index (ft) |
|---|---|---|---|---|---|---|---|
| Entire Highlands | 50.8 | 78 | 122.2 | 19.9 | 838 | 58.1 | 69.2 |
| Connecticut | 71.3 | 76 | 104.0 | 17.7 | 720 | 55.4 | 64.9 |
| New York | 57.9 | 94 | 103.7 | 19.8 | 898 | 55.8 | 66.5 |
| New Jersey | 62.5 | 80 | 123.5 | 20.4 | 874 | 60.0 | 64.8 |
| Pennsylvania | 34.4 | 72 | 132.1 | 22.1 | 916 | 60.4 | 80.3 |
| Highlands N of glacial margin | 69.1 | 83 | 114.0 | 18.4 | 784 | 56.1 | 63.7 |
| Highlands S of glacial margin | 35.5 | 72 | 131.1 | 21.4 | 911 | 59.1 | 78.3 |

* Gross cubic feet of wood in an average tree > 5 in (12.7 cm) diameter.
** Total aboveground oven dry weight in lb of an average tree 1 in (2.54 cm) diameter or larger.

began to substantially alter Highlands forests early in the twentieth century, starting with the loss of American chestnut to the Asiatic chestnut blight fungus (*Cryphonectria parasitica*). Subsequently introduced "pests" and pathogens greatly reduced American elms (*Ulmus americana*) and populations of several other native species. Many nonnative taxa have now become widespread and essentially "naturalized" in Highlands forests.

Currently about half of the Highlands region from Pennsylvania to Connecticut features forest cover (see plate 11), far less than the amount of pre-European forest cover but nearly twice as much as a century ago. Most modern forests are substantially fragmented, and the great majority are composed of individual small tracts. Highlands forests range from very young, early successional woodlands to mature forest communities up to about 150 years of age. The average age of 551 forest stands in the Highlands study area was 78.1 years, as recorded by FIA inventories between 2003 and 2008, with an average tree height of about 58 feet (17.7 meters). Well-developed forests in the Highlands have four more-or-less distinct vegetative strata: canopy, understory, shrub layer, and ground layer. Along with these four strata, numerous niches and microsites support a diverse assemblage of organisms. However, young stand age and shallow soils limit the height of many Highlands forests. Basal area of stands (the cross-sectional area of a tree measured at chest height, in this case summed across a group of trees) around the region averages 122 square feet per acre (28 square meters per hectare) with an average tree aboveground dry biomass of 838 lb (380 kg) and an average wood volume of 19.9 cubic feet (0.56 cubic meters; see table 7.1). On those areas with sufficient wood-producing capacity to be classified as timberland, the average timber tree contains about 10.5 cubic yards (8 cubic meters) of wood.



Embedded within the oak-dominated matrix in wetlands, along streams, and in flat areas with high soil moisture are found more hydrophytic forest communities characterized by trees such as red maple, shagbark hickory (*Carya ovata*), and American sycamore (*Platanus occidentalis*). Air temperatures on north-facing Highlands slopes and ravines can be several degrees cooler than on nearby south-facing slopes, and growing seasons can be as much as two weeks shorter. Some of these areas feature "northern hardwood" forest communities (variously characterized by white pine, eastern hemlock, sugar maple, beech, and yellow birch (*Betula alleghaniensis*). Differences in composition and structure also occur across the margin between the glaciated (northern) and the unglaciated (southern) sections of the Highlands, due in many cases to different soil conditions and/or contrasting land use histories (table 7.1).

## North of the Glacial Margin

Most of the Highlands region north of the glacial margin is composed of rugged uplands with as much as 1,310 feet (400 meters) of local relief (see plate 12). Forest cover averages nearly 70 percent, and parks and preserved lands are common. Slopes are frequently steep with shallow, acidic, till-derived soils underlain by bedrock interspersed with rock outcrops. These conditions are more suitable for the growth of some species (e.g., chestnut and scrub oaks [*Q. illicifolia*], pitch pine) than others. Owing to the natural tendency of fires to burn uphill, upper slopes and ridges have experienced the most fires, and many now feature a high proportion of relatively fire-resistant chestnut oak. Many lower-elevation forests are former farmlands colonized by red and sugar maple, beech, hickories, basswood (*Tilia americana*), and oaks. In a few scattered valley areas where soils developed from calcareous materials, the higher pH has favored a different suite of tree species (e.g., eastern red cedar [*Juniperus virginiana*], American elm, white ash [*Fraxinus americana*], sugar maple), although most of these areas with better soils remain cultivated.

The New Jersey Highlands north of the glacial margin are 69 percent forested, with the oldest average stand age among the states at eighty-three years. White oak/red oak/hickory; yellow poplar/white oak/red oak; and chestnut oak are the most common local cover types. Upland forest understory typically features witch hazel (*Hamamelis virginiana*), mountain laurel (*Kalmia latifolia*), huckleberry (*Gaylussacia* spp.), and blueberry (*Vaccinium* spp.). Proceeding north from the glacial margin, New Jersey uplands exhibit increasing slope, more oak and less maple, and a decreasing proportion of developed land. According to FIA countywide data for all counties within the Highlands study area, the proportion of productive "timberland" peaks in Sussex County at more than 50 percent. The western Highlands in New Jersey and adjacent New York contain some of the region's most important contiguous, protected forests, with many tracts larger than one thousand acres. Between the glaciated uplands, Highlands valleys in New Jersey average 45 percent forestland and 30 percent developed land. Many valley forests are young woodland mixes of black cherry (*Prunus serotina*), red maple, and early successional and invasive species, while others are dominated by tulip poplar and sugar maple. These valley forests are often quite fragmented and contain many nonnative species but are capable of developing great stature and complexity.

New York's Highlands region, in contrast, is only 58 percent forested and is dominated by red oak; chestnut oak/black oak/scarlet oak (*Q. coccinea*); and red maple/lowland hardwoods forest types (table 7.1). Some higher-elevation and north-facing slopes in New York (as well as New Jersey) feature hemlock–northern hardwood forests with eastern hemlock, sugar maple, and occasionally American beech as well as associated trees such as yellow birch and striped maple (*Acer pensylvanicum*). A pitch pine/oak/heath community type (dominated by pitch pine, chestnut oak, and scrub oak) is sometimes present at higher elevations and on ridgetops. Forested wetlands are common and are typically dominated by red maple with other trees such as black ash (*Fraxinus nigra*) and bitternut hickory (*Carya cordiformis*), and a dense layer of shrubs such as spicebush (*Lindera benzoin*), black chokeberry (*Aronia melanocarpa*), and highbush blueberry (*Vaccinium corymbosum*). Mesic forests in lower elevations may also have elm, tulip poplar, and sugar maple. Putnam and Dutchess counties are heavily forested and over half covered in timberland while the Highlands in Rockland and Westchester counties (closer to New York City) feature more than 50 percent developed land. New York's Highlands forests have the lowest average basal area among the four states at less than 104 square feet per acre (23.8 square meters per hectare).

The Connecticut portion of the Highlands is more than 71 percent forested (table 7.1) and includes many parks and preserved lands. Common local forest types are white oak/red oak/hickory; red oak; and sugar maple/American beech/yellow birch, with significant areas of white pine and eastern hemlock forest (see plate 13). More than half of Litchfield County is productive timberland with a high volume of sawlog trees. The easternmost portion of the Connecticut Highlands study area lacks the oak dominance and bedrock outcrops characteristic of the central Highlands. The commonness of paper birch (*Betula papyrifera*), yellow birch, and understory shrubs such as nannyberry (*Viburnum lentago*) attests to the cooler northern climate of these forests.

## South of the Glacial Margin

The Highlands south of the glacial margin are generally less steep and less rocky and feature less local relief and more fertile soils. Uplands cover less area than the surrounding lowlands and valleys, and the remaining forest



tracts occur within a matrix of predominantly developed or cultivated lands. The area features few contiguous forests larger than one thousand acres (405 hectares), and fewer parks and preserved lands than the northern Highlands. Forest cover averages 35.5 percent, or just more than half of that north of the glacial margin, and the stands are on average eleven years younger (table 7.1). Despite their younger age, the trees are taller on average than in the northern Highlands, and stands have higher average basal area and aboveground biomass compared to stands north of the glacial margin, reflecting generally more productive growing conditions. The most common local cover types are yellow poplar; yellow poplar/white oak/red oak; white oak/red oak/hickory; and red maple/oak. From New Jersey south through the Pennsylvania Highlands there is a trend of decreasing amount of forest cover, smaller tracts, increasing fragmentation, and less preserved and protected forestland.

The New Jersey Highlands south of the glacial margin are 48 percent forested, with high basal area, wood volume, and biomass. The most common local forest type is yellow poplar/white oak/red oak. Uplands are 58 percent forested and feature white and black oak (*Q. alba* and *Q. velutina*) with red oak, red and sugar maple, and white ash. Areas between the ridges have deep, well-drained soils often enriched by limestone bedrock. As a result, they have high agricultural resource value and are predominantly cultivated, with only 22 percent forestland. Compared to the ridges, valley forests south of the glacial margin feature less oak and more yellow poplar and black birch (*Betula lenta*).

In the Pennsylvania Highlands, Reading Prong bedrock is widely dispersed, and Highlands forests are scattered and often highly fragmented. Only 34 percent of the land is forested: Bucks, Montgomery, and Lancaster counties are less than 25 percent forested, and all other Highlands counties are less than half forested. A matrix of cultivated lands surrounds most remaining forests, interspersed with towns and developments. The uplands rise generally only 300–650 feet (100–200 meters) above surrounding lowlands and valleys. Average stand age is the youngest among the Highlands states at seventy-two years. However, site index and productivity are high with good sawtimber volume in Northampton, Chester, and Lancaster counties. Forest cover types are diverse; oaks are less dominant than elsewhere in the Highlands, and hardwoods such as tulip poplar, black gum (*Nyssa sylvatica*), and black walnut (*Juglans nigra*) are more common (see plate 14). The slightly warmer climate favors some species with mostly southern distributions (e.g., catalpa [*Catalpa bignonioides*], black gum) and fewer conifers and northern hardwood species. In the understory, blueberries and huckleberries are less common than in the northern Highlands while shrubs such as spicebush and vines such as greenbrier (*Smilax rotundafolia*) and poison ivy (*Rhus toxicodendron*) are more common.

## Productivity and Diversity

All the diverse forms of life in the Highlands depend on the capture of solar energy by trees and other photosynthetic organisms. Net primary production (NPP) is the annual energy produced by photosynthesis minus that consumed in autotrophic respiration, and it represents the maximum energy available to support ecosystem food webs. Primary production can vary substantially from year to year and certainly varies spatially around the Highlands region. Measurements of net primary production in Highlands forests are relatively rare, but reported values of aboveground NPP for other temperate forest ecosystems range over an order of magnitude, from 0.2 to 1.9 lb per square yard per year (105 to 1,030 grams per square meter per year), with soil moisture, nitrogen availability, temperature, and light viewed as major controlling factors (Kloeppel, Harmon, and Fahey 2007). NPP can play a key role in regulating the size of animal populations and community biomass and can influence levels of biological diversity. Primary production is directly important to humans through impacts on wood production and the sequestration of atmospheric carbon dioxide.

Primary production in forests results in commodities such as timber, fuelwood, pulp, fruits, nuts, and greenery. Through much of the twentieth century, rates of timber removal in the Highlands were fairly low as cultivated lands returned to forest and many young forests matured. During the 1980s and 1990s the annual net growth of sawtimber and growing stock was more than twice the rate of wood removal (Phelps and Hoppe 2002). Highlands counties with the highest current volumes of sawtimber (more than five thousand board feet per acre of forest) include Connecticut's Litchfield and Hartford counties, Dutchess and Putnam counties in New York, all the New Jersey Highlands counties, and Chester and Lancaster counties in Pennsylvania. Since many trees in these forests are now reaching sawtimber size, a future increase in logging, especially for valuable oaks on private lands, is likely to occur. The 2002 Highlands regional study update concluded that half of all forest owners expect to harvest wood products in the future (Phelps and Hoppe 2002).

The regrowth of many eastern Northern American forests following extensive forest clearing in the 1800s resulted in a globally important carbon sink, slowing the rate of atmospheric $CO_2$ increase, thus forestalling associated climate consequences (Pacala et al. 2001; Myneni et al. 2001). Long-term data from New York's Black Rock Forest document that carbon stored in aboveground biomass nearly tripled between 1930 and 2000 (Schuster et al. 2008) (fig. 7.1). The period of highest long-term increase was from the 1930s through the early to mid-1960s, with an average annual increment of 2,675 lbs/acre (approx. 3 metric tons/hectare) of biomass. Red oak trees sequestered carbon during that period three times faster than most other species.



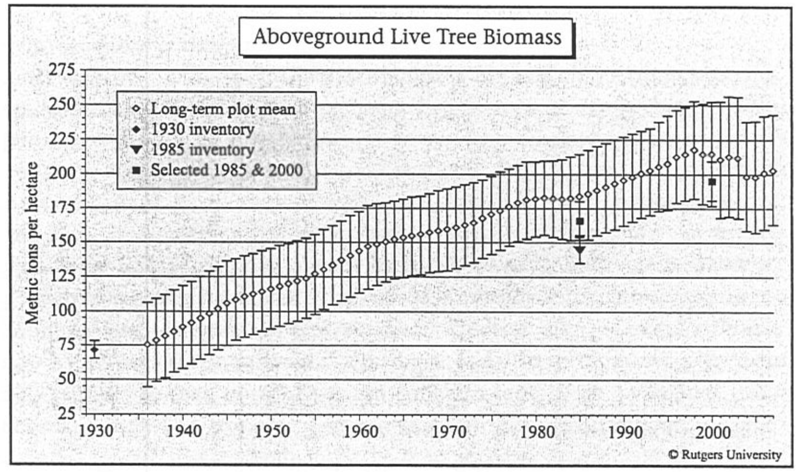


*Figure 7.1.* Forest-wide aboveground live tree biomass (AGB in metric tons/hectare) in the Black Rock Forest as estimated in 1930 and 1985 inventories, mean AGB from a subset of 45 inventory plots in 1985 and 2000, and mean AGB on a series of long-term plots from 1936 to 2006. *Source:* Black Rock Forest/Schuster et al. 2008 © Rutgers University.

However, the capacity of forests to store carbon is sensitive to factors including stand age, climate, and disturbance. Some of Black Rock's maturing forests exhibited decreasing annual carbon storage after the 1960s, although other stands more than one hundred years old exhibited undiminished biomass increments (Schuster et al. 2008). Periods of widespread slow growth (1946–1954, 1960–1966, and 1979–1986) were associated with droughts and outbreaks of insect herbivores. Recently in the Black Rock Forest and elsewhere in the Highlands, there has been a wave of tree mortality, notably on poor sites between 1999 and 2005, which reduced live carbon stocks by as much as 15 percent (see fig. 7.1; Schuster et al. 2008).

The drought-prone and nutrient-poor soils that characterize many Highlands uplands limit levels of primary productivity. This is evident in the low biomass-to-stand-age ratios in Highlands regions with higher proportions of upland habitat (table 7.1). There is also a general north-to-south increase in productivity correlated with increasing temperature and growing season length and generally higher soil productivity. Some areas have lower productivity due to human-caused erosion or soil compaction. The forests with the highest productivity per acre are all south of the glacial margin (Hunterdon and Morris counties in New Jersey and Bucks and Berks counties in Pennsylvania; table 7.1).

The high habitat diversity of the Highlands (e.g., wetlands, ravines, ridges, rocky summits, talus slopes, outcrops) and the persistence of some large contiguous forest tracts have resulted in high overall biological diversity. Species diversity is generally highest in undisturbed forests with a range of habitats but can also be high in young forests with mixtures of early- and middle-successional native and nonnative species. Woody plant diversity can be locally quite high. For example fifty species of trees occur within the 3,830-acre (1,550 hectare) Black Rock Forest, and it has more than one hundred woody plant species overall (Barringer and Clemants 2003). Regional habitat and species diversity are also enhanced by the Hudson and Delaware rivers and the long, continuous ridges of the Highlands, which act as natural north–south biotic corridors.

Challenges to native species diversity in the Highlands include the absence of truly old forest and the rapid expansion of some aggressive, predominantly nonnative organisms. Some characteristic species have been eliminated across the region (e.g., American chestnut, timber wolf), and others remain seriously threatened. Disturbance often confers competitive advantages to weedy, light-loving species that can outcompete native forest species for critical resources. Plants such as Japanese barberry (*Berberis thunbergii*) and stilt grass (*Microstegium vimineum*) have specialized adaptations that enable them to thrive in areas of disturbance and tree mortality (Xu, Griffin, and Schuster 2007; Xu, Schuster, and Griffin 2007). Other abundant, invasive, nonnative plants in the Highlands include common reed (*Phragmites australis*), introduced honeysuckles (*Lonicera* spp.), purple loosestrife (*Lythrum salicaria*), Japanese bamboo (*Polygonum cuspidatum*), and garlic mustard (*Aliaria petiolata*). Even in the relatively undisturbed Black Rock Forest, introduced plants represent 20 percent of the flora (Barringer and Clemants 2003). Introduced animals that have spread throughout the Highlands include brown-headed cowbirds (*Molothrus ater*), which parasitize the nests of many forest-interior breeding birds, and the hemlock woolly adelgid insect (*Agelges tsugae*), which has devastated eastern hemlock populations.

Forest ecosystem trophic (food web) structure has been altered for more than a century owing to the aforementioned extirpation of top predators, essentially "decapitating" food webs. Large predators have not become re-established in much of the Highlands region. Some herbivore species, thus released from "top-down" population regulation, have increased severalfold, resulting in widespread problems. White-tailed deer (*Odocoileus virginianus*) populations are especially imbalanced near populated areas where hunting is restricted. Humans are affected by overabundant deer as they damage domestic plants and agricultural crops, cause motor vehicle accidents, and serve as vectors for the spread of Lyme disease. Excessive deer are a major wildlife concern because they heavily consume acorns and food resources critical for many other animals. Excessive deer browse on seedlings, combined with heavy consumption of acorns, severely disturbs tree regeneration and community dynamics, threatening the future of many oak forests (Loftis and McGee 1992; Townsend et al. 2002; Tripler et al. 2005). This process has been shifting forest composition from preferred and browse-sensitive species to less preferred and nonbrowsed species (Romagosa and Robison 2003; Harrison and Bardgett 2004; Haas and Heske 2005). Most Highlands forest understories no longer feature the same species as the overstory, portending very different future forests (fig 7.2). FIA data for Pennsylvania indicate that one-half to two-thirds of the state's forests lack sufficient tree seedlings to regenerate these forests (McWilliams et al. 2002). Where deer populations are excessive, regeneration of native shrubs is also threatened, and populations of sensitive wildflower species have been reduced or lost completely. Areas where deer exclosures have been erected clearly document the impacts of large mammal browse on forest productivity, diversity, and regeneration. Some improvement of the situation may result from increasing populations of coyote (*Canis latrans*) and black bear (*Ursus americanus*) where sufficient forest habitat remains to sustain them.



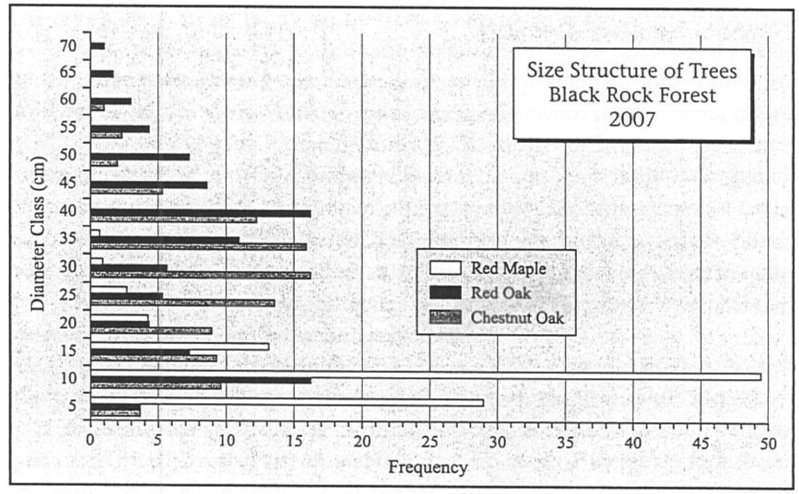


*Figure 7.2.* Size structure (percent frequency) of trees of three species in the Black Rock Forest showing typical paucity of small saplings. Note the small numbers of red and chestnut oak of the smallest size class of saplings (< 5 cm in diameter), which suggests future problems with successful oak regeneration.

## Biogeochemical Cycling

All nutrients cycle between living organisms and the abiotic environment. Forest ecosystem productivity and health depend on these biogeochemical cycles to provide nutrients for uptake and growth. Cycling rates and nutrient availability vary widely around the Highlands, partially explaining differences in NPP. Because water is the medium in which most nutrients move, watershed inflows and outflows of these nutrients can be examined to compile biogeochemical budgets, which serve as indicators of ecosystem function and change over time. Healthy forest ecosystems typically exhibit tight, local cycling of key nutrients such as nitrogen and calcium, with minimal export in soil and stream waters (Bormann and Likens 1979; Aber et al. 2001). The major labile reservoirs of these nutrients are usually contained in organic materials, including the forest biota. Low nutrient availability in some Highlands soils can limit growth, especially in uplands with shallow soils over crystalline bedrock. In comparison, deeper soils, and especially those developed from calcareous materials or on alluvial deposits, feature higher availability of most nutrients.

Several other factors affect forest nutrient cycling and uptake. Periods of drought, especially where soils have low water-holding capacity, reduce water and nutrient uptake. Land use can substantially affect soil nutrients, with long-lasting implications for productivity and diversity (Dupouey et al. 2002). Agricultural practices can reduce soil organic-matter content by as much as 30 percent (Compton et al. 1998) and can also cause soil nutrient loss and increased erosion (Entry, Sojka, and Shewmaker 2002). The availability of nitrogen required for forest regrowth depends on the intensity of the previous agriculture, with recovery taking decades in some heavily farmed areas (Compton et al. 1998; Hooker and Compton 2003).

Forest species composition can also affect nutrient cycling (Elliott, Elliott, and Wyman 1993; Gartner and Cardon 2004). Many oaks have unique foliar and litter qualities that affect carbon and nitrogen cycling, slowing decomposition and nitrification (Finzi, Van Breemen, and Canham 1998; Lovett et al. 2004) and increasing the retention of atmospherically deposited nitrogen (Templer et al. 2005; Lovett et al. 2004). In contrast, sugar maple and white ash produce soil organic matter with low C:N ratios and high nitrification rates (Finzi, Van Breemen, and Canham 1998). The replacement of native plant species with nonnative species such as Japanese barberry can also alter forest chemical cycling and soil microbial communities (Kourtev, Ehrenfeld, and Haggblom 2002; Kourtev, Ehrenfeld, and Huang 1998). The expansion of invasive plants and the northward migration of some native forest taxa such as mulberry (*Morus rubra*) and black gum may have biogeochemical consequences deserving of further research.

Forest fires can act to enhance nutrient cycling, while fire suppression



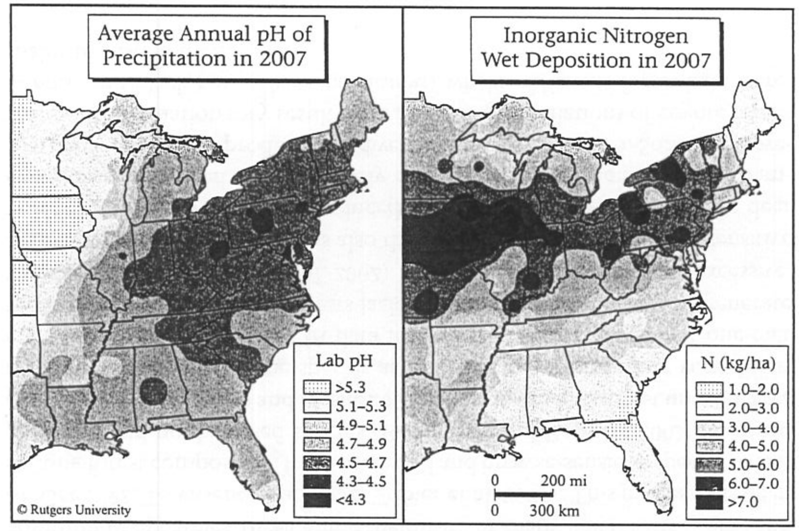


*Figure 7.3.* (*Left*) Isopleth map of average annual pH of precipitation in 2007 at National Atmospheric Deposition Program sites around the eastern United States. (*Right*) Isopleth map of total inorganic nitrogen deposition in precipitation in 2007 at National Atmospheric Deposition Program sites around the eastern United States. © Rutgers University.

generally retards cycling rates. But when forest canopy trees are lost to disturbance, nutrients may be leached from soils, especially if there is a lag before other trees respond with increased growth (see, e.g., Jenkins, Aber, and Canham 1999). Disturbances that reduce woody plant transpiration will at least temporarily increase soil water levels, potentially resulting in nutrient losses through leaching. Forest clear-cutting without environmental controls has been shown to trigger massive losses of nutrients (Bormann and Likens 1979). Losses of soils and nutrients from forests can dramatically reduce productivity and water quality at the same time.

A prominent feature of Highlands forest biogeochemistry is widespread soil and ecosystem acidification, with the severity inversely proportional to local acid-neutralizing capacity. Precipitation in the northeastern United States has been especially acidic since the industrial revolution, and the pH of Highlands precipitation is typically between 4.0 and 5.0 (see fig. 7.3; Shapiro 2005; Shapiro et al. 2007). Acid deposition can lower soil pH over time, causing nutrients such as nitrogen, calcium, and magnesium to bind more tightly to soil particles, reducing their availability. In highly acidified soils, aluminum availability may reach toxic levels, and aluminum may be released to stream waters (Shortle et al. 1995). Some upper watershed areas in the Highlands have become heavily acidified, resulting in strong selection for the most acid-tolerant species, such as gray birch (*Betula populifolia*).

Substantial quantities of nitrogen accompany the hydrogen ions in acid precipitation, potentially leading to forest degradation through nitrogen saturation (Aber et al. 2001). Acid precipitation in the Highlands deposits more than 4.5 lbs of nitrogen per acre per year (5 kilograms per hectare per year) (see fig. 7.3; NADP 2007), and the amount of additional "dry" deposition may be similar in magnitude (Shapiro 2005). Atmospheric inputs of nitrogen may become immobilized in soils or taken up by plants. In some cases, however, nitrogen may be exported in stream waters, especially in steep areas and during winter and early spring when biological demand for nitrogen is very low. Where nitrogen is found in any quantity in stream water, it generally indicates a problem (Aber et al. 2001). However, oak forests usually feature strong nitrogen retention (Lovett, Weathers, and Arthur 2002), and streamflow from undisturbed Highlands forests is most often very low in nitrogen.

Excess hydrogen ions from acid deposition can displace positively charged ions such as calcium, magnesium, and potassium from soil exchange sites, lowering base saturation and accelerating acidification (Likens, Driscoll, and Buso 1996; Hyman et al. 1998). Nutrient depletion from any cause (e.g., acid leaching, disturbance, heavy agricultural use) can increase forest susceptibility to a range of climatic and biotic stresses. Tree health problems can include increased vulnerability to winter injury, crown dieback, and exacerbated impacts from herbivory or disease (Lovett et al. 2006). Widespread declines of sugar maple have been linked to acid depletion of soil cations (Likens, Driscoll, and Buso 1996; Long, Horsley, and Lilja 1997; Driscoll et al. 2001). Nutrient depletion and associated tree stress can result in reduced growth and timber yield, increased mortality rates, and eventual changes in forest composition and diversity.

## Disturbance Dynamics

Among the changes occurring in Highlands forests has been the alteration of disturbance regimes. Eastern deciduous forests typically cycle from open woodlands to middle-aged closed-canopy forests to old forests as shorter-lived species requiring high light are replaced by slower-growing, shade-tolerant trees with longer life spans. Disturbances such as fires, ice storms, and large windthrow events occur with characteristic frequencies, intensities, durations, and extents. These parameters of the disturbance regime determine the proportion of forest stands in any given successional "stage." Sooner or later, all stands in all forests are reset to earlier stages by disturbance.

Young Highlands forests are usually dominated by fast-growing species such as gray birch, pin cherry (*Prunus pennsylvanica*), and aspen (*Populus* spp.). These trees are eventually replaced by longer-lived species such as most of the oaks, and these in turn may eventually be replaced by the region's most shade-tolerant and long-lived taxa, such as sugar maple, beech, and hemlock. But in most of the Highlands, and a much larger surrounding area, characteristic disturbance regimes have enabled oaks to dominate for most of the last ten thousand years (Abrams 1992; Maenza-Gmelch 1997). Indeed, oak-dominated forests are the most widespread type of forest in the eastern United States.



Human activities have figured in Highlands disturbance regimes for most of the Holocene, through direct tree cutting and land clearing as well as impacts on fire dynamics. Other natural disturbance factors include windthrow, ice storms, regional droughts, flood events, and insect and disease outbreaks at irregular intervals. The natural fire regime of Highlands forests features small fires, usually ground fires that reduce fuel loads and release nutrients, and occasional larger fires during extremely dry periods that can cause widespread tree mortality, favoring fire-adapted species. These conditions have supported the regeneration of oak forests. Fire frequency appears to have increased dramatically in the Highlands following European settlement (Maenza-Gmelch 1997). Many of these fires were of low intensity and extent, but when combined with accumulated, fire-prone logging debris and dry conditions, fire intensity was occasionally high and extended over large areas. In addition to oaks, this fire regime favored most species of birch and pine at the expense of species such as sugar and red maple, beech, and hemlock. The effects on forest composition were most pronounced in frequently burned upper slope and ridge communities. Highlands fire disturbance regimes were substantially altered by the implementation of active fire suppression in the twentieth century. Fire frequency decreased dramatically afterward, and fire suppression continues to this day. Over time, in the absence of fires, oak seedlings and saplings are often outcompeted by fast-growing, fire-sensitive species such as thin-barked red maple (Chapman, Heitzman, and Shelton 2006; Drury and Runkle 2006). However, fire suppression can also lead to substantial fuel-load buildup, which potentially increases the intensity of future fires.

As a result of these changing disturbance factors, and especially owing to the historical legacy of widespread clearing followed by land-use abandonment, today's Highlands forests are overwhelmingly middle-successional. Most current stands originated between 1900 and 1960, with 85 percent of stands in the range of 40–100 years old (see fig. 7.4). Some fragments of older hemlock/beech, chestnut oak, and white oak forest up to 150 years old still remain, and individual trees can be found with ages of 200–300 years (e.g., D'Arrigo et al. 2001). But very little true old growth remains anywhere in the Highlands.

Disturbances from outbreaks of so-called forest pests and pathogens, including both native and introduced organisms, have had major impacts on these forests through history. But their rates of introduction and spread have increased in recent times, in part a consequence of increased human travel.

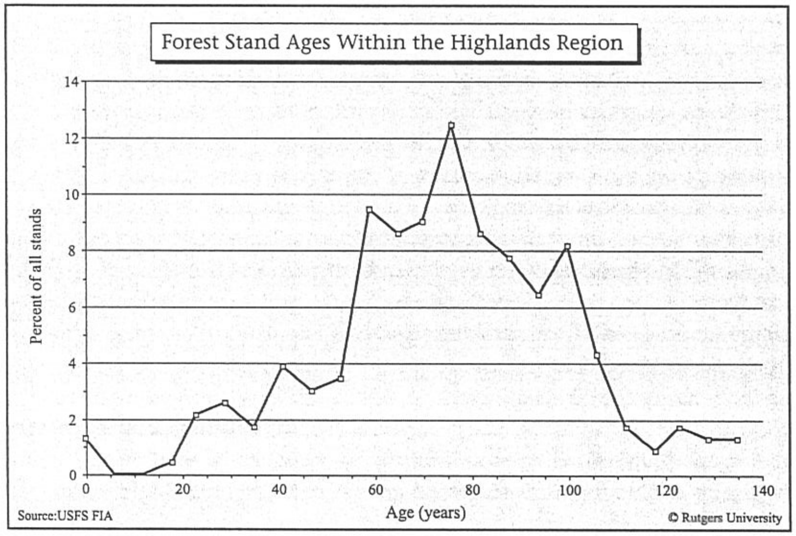


*Figure 7.4.* Distribution of forest stand ages among U.S. Forest Service Forest Inventory and Analysis stands within the Highlands region. © Rutgers University.

Pests and pathogens can have significant short- and long-term impacts on forest ecosystem processes such as productivity, nutrient cycling, and support of food webs. These were undoubtedly affected by the earlier pathogen-induced losses of American chestnut and American elm. Lovett and colleagues (2006) stated that "exotic insect pests and pathogens pose the most serious current threats to forests of eastern North America." The most critical biological features determining the severity of pest and pathogen outbreaks are virulence, mode of action, host specificity, and importance or uniqueness and phytosociology of the host tree (Lovett et al. 2006). Some hardwoods and conifers termed "foundation species" play particularly critical roles in regulating hydrology, fire, carbon storage, and nutrient cycling in temperate forests (Pastor and Post 1986; Houghton and Hackler 2000; Foster et al. 2002; Lovett, Weathers, and Arthur 2002; Lovett et al. 2004; Templer et al. 2005). Pest and pathogen impacts on these foundation taxa can dramatically alter ecosystem function and services (Ellison et al. 2005).

The hemlock wooly adelgid (HWA)—an introduced, foliage-feeding insect that specifically targets "foundation" eastern hemlock trees—meets the worst-case scenario for the above-listed severity factors. Highlands stands of eastern hemlock have already experienced as much as 80 percent tree mortality since the insect was first noted in this region in the 1980s (Kimple and Schuster 2002). Loss of this dominant evergreen from eastern forests is accompanied by ecological changes that affect plant, animal, and fungal populations and alter soils, diversity, trophic structure, and ecosystem processes (Jenkins, Aber, and Canham 1999; Danoff-Burg and Bird 2002; Tingley, Orwig, and Field 2002; Lewis et al. 2008). Hemlock stands provide critical winter habitat for white-tailed deer, ruffed grouse (*Bonasa umbellus*), and wild turkey (*Mealeagris gallopavo*) (McWilliams and Schmidt 1999). Hemlock loss can lead to increased stream temperatures and algae growth, which can harm aquatic invertebrates, fish, and salamanders in steams and riparian zones (Snyder et al. 2002; Brooks 2001). Eastern hemlock stands are the preferred habitat of the Canada warbler (*Wilsonia canadensis*), the hermit thrush (*Catharus guttatus*), the magnolia warbler (*Dendroica magnolia*), the solitary vireo (*Vireo solitarius*), and the black-throated green warbler (*Dendroica virens*), whose populations in Connecticut declined precipitously after hemlock mortality from HWA (Mitchell 1999; Tingley, Orwig, and Field 2002).



Significant biotic challenges are now being faced by other forest taxa that have been resilient to past perturbations. Beech bark disease, for example, is a multiorganism complex currently spreading south through the Highlands. It affects American beech trees by reducing growth and vigor, eventually leading to mortality in many trees (Houston and O'Brien 1983). Butternut canker, resulting from a fungus (*Sirococcus clavigignenti-juglandacearum*) first introduced into the United States about fifty years ago (Anderson and LaMadeleine 1978), has already killed most of the butternuts (*Juglans cinerea*) through the region. Many Highlands ash trees have been weakened and in some cases killed by "ash yellows," an incurable disease caused by a single-celled mycoplasm (Matteoni and Sinclair 1985). Emerald ash borer (*Agrilus planipennis*), a wood-boring beetle introduced from Asia that is lethal, fast acting, and specific to ash trees, is now spreading east toward the Highlands area (Tkacz, Moody, and Castillo 2007). Sugar maple trees have been killed in the New York metropolitan region by the Asian long-horned beetle (*Anoplophora glabripennis*), an introduced wood-boring insect that preferentially attacks maples but will also damage other hardwoods.

Pathogens that now threaten eastern oak forests include oak wilt fungus (*Ceratocystis fagacearum*), spreading toward the Highlands from the west, and bacterial leaf scorch (caused by *Xylella fastidiosa*), presently expanding into New York from New Jersey. Of possible future concern is *Phytophthora ramorum*, the pathogen that causes "sudden oak death" (SOD). After outbreaks of this water mold, large numbers of oak trees exhibit trunk bleeding and bole lesions, often resulting in death (Hansen, Parke, and Sutton 2005). SOD has killed hundreds of thousands of oak and tan oak trees in near-coastal locations in California and Oregon (USDA 2005), and eastern red and white oaks have both shown susceptibility to *P. ramorum* in greenhouse trials (Brasier et al. 2002; Tooley and Kyde 2003). Moreover, modeling results indicate that much of the eastern deciduous forest may be susceptible to SOD (Meentemeyer et al. 2004; Magarey, Fowler, and Randall-Schadel 2005). The USDA's "National Strategic Plan for Sudden Oak Death" states, "The oak hardwood forest is the largest forest type in the U.S., and its potential vulnerability to this pathogen is of considerable economic and ecological concern" (USDA 2005).

Many aging Highlands oak canopy trees are stressed by changing soil and climate factors and may be senescing or becoming increasingly prone to disease. Recent studies have documented an unexplained tripling of oak tree mortality and a 15 percent loss of oak canopy biomass in the Black Rock Forest since 1999 (Schuster et al. 2008). The phenomenon is consistent with "oak decline," the name for a slow-acting complex usually involving environmental stress combined with the effects of pests or pathogens, or both (Wargo, Houston, and LaMadeleine 1983). Drought often appears to be an initiating agent, and water-stressed trees become more susceptible to stem-girdling *Armillaria* fungi, which usually feed only on dead tree roots. Defoliating insects can also trigger the disease complex.

Regardless of the mode of canopy tree loss, the future of oak forests is uncertain because of widespread regeneration failure. Older oak trees have reduced propensity to sprout successfully after cutting, and overherbivory resulting from trophic imbalance, combined with fire suppression, has nearly eliminated oak regeneration by seedlings. Loss of oak forest may lead to a range of ecosystem effects such as water-quality deterioration (Lewis and Likens 2000; Lovett, Weathers, and Arthur 2002; Templer et al. 2005). Forest diversity—including animals, microbes, and subcanopy and understory plants—may be significantly affected by oak loss, potentially changing ecosystem processes if functional diversity is also altered. Losses of close associates of oaks, such as specialist ectomycorrhizal fungi and insects, will be expected, and many other insects, birds, and vertebrates that feed on oak tissues may respond negatively as well. Acorns are a critical food resource for birds and mammals during the dormant season, used to build fat reserves for winter survival, which will not be easily replaced by other foods. Loss of oak mast may prove devastating to oak-adapted wildlife, altering food webs for decades (Ostfeld, Jones, and Wolff 1996; McShea et al. 2007). Elements of the Highlands forests' disturbance regimes and their relative impacts continue to change over time, with many implications for future forest composition, structure, and ecosystem processes.

## Highlands Forests and the Future

Forests act as ecological life-support systems, and humans have depended on Highlands forests for a wealth of products and supporting services over the past centuries. Chief among these has been the purification and provision of



large quantities of water. Forest vegetation, roots, and litter protect soils and watersheds, control stream siltation and sedimentation, filter pollutants, and replenish groundwater. Forests also scavenge air pollutants and release much of the oxygen that humans and other resident animals breathe. They provide valuable commodities including timber and fiber, foster soil development, control local cycling of nutrients, and function in global cycles of water, carbon, and other chemicals (Dixon et al. 1994). They provide climate control and support a wealth of wildlife and biological diversity. The Highlands are particularly valued for recreation and nature enjoyment, enhancing human health, and for beautifying the landscape. But Highlands forests face a number of challenges to their health and their ability to continue to provide these ecoservices.

Only about half of the Highlands landscape is currently forested; most of these forests are highly fragmented, and many face continuing development pressure. Ongoing challenges include suppression of the natural fire regime; further ecosystem acidification and other biogeochemical changes; widespread displacement of native species by exotics; canopy tree stress and mortality from pests, pathogens, climatic stresses, and senescence; and likely future increases in logging concurrent with widespread forest regeneration failure. Highlands forests may also conceivably experience future reductions in soil and forest productivity, waves of species mortality, or loss of function as carbon sinks. Not all areas will experience all these impacts, and some will prove resistant to certain changes. But even some large, preserved Highlands forests are already experiencing a number of these impacts, and some heavily fragmented forests exhibit diminished ability to provide critical services, such as yielding clean water.

Interactions among these factors may further augment the challenges. For example, although growing conditions are generally good south of the glacial margin, this part of the Highlands faces high development pressure, which may bring further habitat loss and fragmentation. These factors combined with regeneration failure and increasing influxes of exotic species may increase the rapidity and magnitude of forest change. Further climatic changes are especially likely to exacerbate impacts of other factors.

The Highlands region experienced an overall warming of winters and summer nights during the twentieth century, with spring arriving earlier and winters becoming less snowy (Warrach et al. 2006). Further warming will especially challenge native species that are sensitive to winter temperatures and the presence or absence of snowpack (Pederson et al. 2004; Pederson 2005) and may result in loss of the region's northern hardwood forest component. Changing climate is already implicated in Highlands community composition changes: most of the species that were extirpated from the Black Rock Forest between 1930 and 2000 were northern relicts (e.g., black spruce [*Picea* *mariana*]), and most of the species that invaded the forest in that time were expanding their ranges from the south (e.g., red mulberry and catalpa; Schuster et al. 2008). Modeling by the U.S. Forest Service projects that if current rates of climate change continue, within the next century the Highlands climate will be unsuitable for native trees such as sugar maple and hemlock but suitable for species such as southern pines, currently growing hundreds of miles to the south (Iverson, Prasad, and Matthews 2007). Productivity, biogeochemistry, and species diversity will all be affected by compositional changes. Future climate-induced range changes will likely depend on actual rates of fossil fuel emissions (NECIA 2006).

Envisioning the Highlands in as little as fifty years into the future—after the current oak canopy is largely gone and in a warmer climate—raises several concerns. There will probably be less forested area. More species will have followed American chestnut and American elm into oblivion, and some forest types, such as northern hardwoods, may disappear from the region. We do not know which species will survive, but eastern hemlock, American beech, ash, and butternut will certainly be greatly diminished, and sugar maple populations may have declined as well. Native trees that may increase in dominance include red maple, black birch, and yellow poplar on sites with better soils. Black gum and southern hickories may increase on warmer sites, and associated species could include southern pines. Invasive trees including tree of heaven, Norway maple, and buckthorn will almost certainly have expanded substantially. These forests will represent novel forest types with uncertain implications for ecological processes and services. A general reduction in wood quality, and thus value, would appear to be a likely consequence of such a turnover. Wildlife will be considerably affected, especially by the replacement of acorns by less nutritious seeds. Many species of organisms may be extirpated, resulting in reduced native species diversity. Nutrient cycling will certainly be affected, with potentially serious consequences for surface water quality. Other implications of such a turnover for human health are uncertain, as are questions of whether these altered forests will support tourism and recreation or will increase land values in the same fashion as today's Highlands forests.

Because so many of the resources, threats, and opportunities are shared among a great many Highlands stakeholders, appropriate and effective responses will necessitate coordinated ecosystem management to conserve and restore forest health and integrity. It will be important to continue to emphasize forest conservation, exemplified by the substantial open-space acquisition and land protection already accomplished in the Highlands through conservation easements since the early 1990s (Phelps and Hoppe 2002). Further incentives that favor forest protection could prove quite beneficial. Given the key role of water in ecological health, it will be especially important to conserve forested wetlands, riparian corridors, and streamside forests. Attention should be given to further reductions of atmospheric pollutant deposition, to active ecological fire management, and to invasive species control. Native carnivore populations should be protected and enhanced, and overabundant deer populations should be reduced through cooperative programs that will restore forests' capacity for regeneration. In this way, more complete ecosystems with diverse and stable food webs may be reestablished. Native species, such as red oak, which store carbon rapidly, conserve nitrogen, and may fare well in the face of climate change (Iverson, Prasad, and Matthews 2007) should be favored and protected. Region-specific guidelines for sustainable forestry should be developed to preserve environmental quality and forest function while ensuring the continued benefits of the provision of forest products. Conservation to maintain reservoirs of native biodiversity in existing forests may provide additional benefits that we cannot yet recognize.



Reestablishment of healthy forests in degraded and heavily damaged areas should also be pursued. Trees of appropriate native species, selected in consideration of climatic and chemical challenges, should be planted in critical areas and protected from herbivory during establishment. Construction of new developments may provide additional opportunities to establish new forests. In areas where existing forest reserves can be augmented, this will serve to increase the long-term viability of native organisms and critical ecological processes, especially where new habitat corridors can be created. Purposeful native species reintroductions could also augment ecological health. Older and newly created forests alike could provide new opportunities for nature tourism, accomplished by means that will support long-term forest viability while still enhancing quality of life and providing local consumable products and other ecosystem services.

It is clear that we cannot re-create the Highlands forests of the past. We also cannot simply preserve current forests and assume that all will remain well. Essentially, we manage nearly every facet of our environment, either by our actions or by our inaction. Deeper understanding will be required to comprehend more fully the relative importance and interactions among the suite of current challenges to Highlands forests, and the consequences for ecosystem health and services. Such an understanding could enable us to develop effective response strategies for future land planning and forest management, to ensure healthy and sustainable forests for the future.

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