Old-Growth Forests:

A Literature Review of the Characteristics of Eastern North American Forests

VERMONT
NATURAL
RESOURCES
COUNCIL
VERMONT'S ENVIRONMENTAL
GUARDIAN SINCE 1963

Old-Growth Forests:

A Literature Review of the Characteristics of Eastern North American Forests

VERMONT NATURAL RESOURCES COUNCIL
VERMONT'S ENVIRONMENTAL GUARDIAN SINCE 1963

July 2005

prepared for
Vermont Natural Resources Council
9 Bailey Avenue
Montpelier, VT 05602

by
Marc Lapin, Ph.D.
Ecosystem Science and Conservation
239 Cider Mill Road
Cornwall, Vermont 05753

VNRC would like to thank Jim Shallow, Stephen Trombulak, and Warren King for reviewing this publication.
We would also like to thank Wallace Global Fund and Ward M. and Mariam C. Canaday Educational and Charitable Trust
for funding this publication and National Life for donating the printing.
Finally, we appreciate the donation of Blake Gardner and Gustav W. Verderber's superb photography.
Captions for Blake Gardner's photographs were taken from *Untamed Vermont,* © 2003 by Thistle Hill Publications.

The Vermont Natural Resources Council, Inc., is a nonprofit environmental organization founded in 1963.
Your support helps fund the continuance of environmental research, education, and advocacy in Vermont.
Join VNRC and receive a subscription to our *Legislative Bulletin* and the
Vermont Environmental Report magazine (both published biannually).

To contact VNRC, please go to vnrc.org or call (802)-223-2328.

Cover photograph by Blake Gardner: **Groton State Forest, Lord's Hill Natural Area:** *Much of Vermont's woodland was cut down for charcoal production, logging, or sheep farming. Few virgin stands remain, but Lord's Hill Natural Area somehow escaped intensive logging. Labeled with tags like museum specimens, the old trees are examples of what was almost lost.*

Foreword

Vermont Natural Resources Council (VNRC) is proud to publish this literature review pertaining to old-growth forests. Old-growth forests are an important part of our natural heritage in the Northeast, and allowing old growth to return to the landscape is integral to our efforts to improve the ecological integrity of Vermont. Even though it will still take hundreds of years to develop true old-growth forest ecosystems, it is an important goal for our region.

VNRC has published this literature review to help educate the public about the characteristics of old-growth forest and its differences with other successional forest stages. This report was developed to contribute to the discussion regarding the ecological role of old-growth forests and their representation on our landscape.

We recognize that all successional forest stages have important roles to play. Wildlife species rely on a mix of habitat conditions ranging from early successional to late successional habitat. Old-growth forests, historically a large part of the northern New England landscape, contribute to biological diversity. In fact, we are still discovering the many ways in which old-growth processes influence our natural world.

This literature review begins the first in a series of technical publications from VNRC in furtherance of our mission to protect Vermont's natural resources and environment through research, education, collaboration, and advocacy. We look forward to sharing additional research and technical expertise to help make informed decisions regarding the stewardship of our natural resources.

— Jamey Fidel
Forest Program Director
Vermont Natural Resources Council

Blake Gardner

Gifford Woods Natural Area: *This National Natural Landmark preserves a small ancient stand of maples that may have been sugared sometime in the last 400 years. With many decaying logs, old-growth trees, and an extensive ground cover of ferns growing from the rich dark earth, these few acres offer a glimpse of what forests looked like before they were removed.*

Introduction

Forests are complex ecological systems consisting of trees, shrubs, herbaceous plants, mosses, liverworts, fungi, soil, water, air, numerous species of microbiota that are invisible to the unaided eye, and animals, from the largest mammals to the smallest insects. Ecosystems are built on interconnection – all the species in a forest are interconnected through numerous pathways such as nutrient and water cycles and predator-prey and plant-herbivore interactions. The species, the physical earth, and the myriad interactions define an ecological system, and because all the parts are fully interconnected, changes to a species, a process, or a characteristic of the soil, air, or water cascade through the forest and lead to other changes.

Old-growth forests, often simply called "old growth," are forest ecosystems that are dominated by old trees and have unique characteristics of stand structure (sizes, ages, spacing of trees) and species composition (including all forms of life), dead wood, and ecosystem function (Barnes 1989, Ontario Ministry of Natural Resources 2003). Old-growth forests also feature disturbance regimes that are natural to the locale and show relatively little human disturbance. Different forest types differ in the way these old-growth characteristics are expressed, but regardless of forest type, old growth has its own unique set of characteristics.

From scientific studies summarized below, the evidence is clear that eastern North American old-growth forest has certain characteristics, species, processes and interactions that either do not occur or are rare in younger forests. Old-growth forests are an element of the natural diversity of life on earth. In the Northeast, old-growth forest ecosystems were the predominant land cover and were the arena where the evolution of species and their ecological interactions took place for thousands of years. As we strive to conserve biological diversity from the scale of genes to ecosystems, it is important that we conserve old growth in its natural spatial pattern – large, continuous expanses.

Changes to a forest ecosystem may be immediate or not apparent for long periods; they may be large and obvious or small and hidden from view. The forests that developed in northeastern North America after the retreat of glaciers over 10,000 years ago went through many changes, due to a gradually changing climate and to the migration of plants and animals from southern non-glaciated lands and northern refugia. In areas of relatively dense Native American populations, such as southern New England, cultural practices changed parts of the forest to a greater degree than in areas where few people utilized the landscape (Whitney 1994). When European settlers entered the forests of New England, they encountered extensive tracts of old-growth northern hardwood, oak-hickory, oak-pine, and spruce-fir forests. In less than half a century in any given region, the forested landscape was transformed to one that was either agricultural or heavily logged. Although much of the forest has regrown from land-clearing and unsustainably intensive logging, the secondary forests are not the same as those that existed previously. The new forests have different proportions of species, and some species have apparently been lost from large parts of the landscape; they have mosaics of habitats that now occur in different proportions and patterns; and they have altered interactions and processes.

The remnant areas of old growth give us clues to the composition, processes and patterns that once dominated the landscape. Despite the scientific inquiry that has examined eastern old-growth forests for at least a century (e.g., Nichols 1913, Harper 1918, Bromley 1935, Jones 1945), eastern North American old-growth forests are ecosystems that are not understood as well as many other forest types. The lack of places where old growth occurs and can be studied, interpreted, and understood, is the primary reason that so little is known about eastern old growth. Only 0.4% of the current forestland in the Northeast is old growth, and no region in the eastern deciduous and mixed forest zone has more than 1.1% old growth (Davis 1996). Nevertheless, the evidence gleaned from old-growth remnants in eastern deciduous or mixed forest and in other temperate forest types clearly indicates that old-growth forests do in many ways differ from their younger counterparts. In order to understand old growth and how it differs, this paper presents a summary of what is known about some of the different species groups of the forest – plants, fungi, insects, mammals, birds, and amphibians. It also discusses parts of forests that go unseen – soil and various interactions that create and maintain the forest ecosystem.

Forest Vegetation – Composition, Structure and Dynamics

Old-growth forest is a stage in a forest's development. In eastern deciduous forest it is characterized, among other things, by an uneven-aged canopy with numerous old, large trees, abundant dead wood, and many canopy gaps. Old growth is not a static end-point in the life of the forest; ongoing growth, death, and disturbances of different types contribute to an ever-changing forest (Tyrell and Crow 1994, Runkle 1998, Runkle 2000, Woods 2000a, 2000b). The "ecological essence" of old growth is continuity – as trees of one generation approach old ages, at about one-half of the maximum longevity of the species, they are replaced by trees of the next generation (Cogbill 1996). Old-growth forests differ from younger stands in many ways, including tree species composition, distribution of tree sizes, number of trees per acre (density), number and sizes of canopy gaps, and dead wood. Even stands that exceed 100 years old and are sometimes described as "mature" differ from old-growth forests.

Tree Age, Size and Density

The canopy of old-growth eastern deciduous and mixed (deciduous-coniferous) forests includes trees of a wide range of sizes and ages; in ecological terminology, the forest is uneven-aged and has diverse structure. Unlike younger and managed forests, a substantial percentage of the canopy trees in eastern and midwestern old-growth forests are greater than 20" diameter at breast height (dbh), and there are many trees that exceed 30" dbh (Nichols 1913, Lorimer 1980, McGee et al. 1999, Hicks and Holt 1999, Abrams et al. 2000, Hura and Crow 2004). Such larger trees are either absent or are very few in younger forests, and that has implications for the habitat of other species and for nutrient cycling, as will be discussed shortly. The oldest-lived species of trees in northern hardwood, spruce-northern hardwood, and hemlock-northern hardwood forests – sugar maple, beech, and hemlock – can live over 300 years; red spruce can exceed 400, and hemlock's maximum age is approximately 600 years (Leopold et al. 1988, Cogbill 1996, Lorimer et al. 2001, Tyrell and Crow 1994).

Since tree size is strongly correlated with tree age, it is those forest elders that represent the large trees that are ever so important for providing the full spectrum of habitats as well as the natural disturbance pattern native to our eastern forests. In the Lake States, where more old-growth northern hardwood forest exists than in New England, researchers found that one-half of the canopy trees in an old-growth forest had attained ages of 200 or greater, and the average time of a tree residing in the canopy was 128 years in sugar maple-dominated forests and 192 years in hemlock-dominated forests (Dahir and Lorimer 1996). In a related study, the average age at death for sugar maple was 215 years and for hemlock 300 years, while the maximum ages recorded were 328 and 513 for the two species respectively (Lorimer et al. 2001). In western Massachusetts, the oldest hemlock in old growth were 300 to 400 years, sugar maple were 200-250 years, and the senior white pine were 200 years old (Dunwiddie 1993, Abrams et al. 2000). Based on tree-age distributions, several scientists have postulated that the transition from mature forest to a later stage with the characteristics of old growth does not occur in northern hardwood and hemlock- or red spruce-northern hardwood types until a stand is 180-215 years old (Cogbill 1996, Dunwiddie et al 1996, Lorimer et al. 2001). When dead-wood characteristics are considered, however, as discussed below, it has been found that 275-300 years are required before old-growth features develop (Tyrell and Crow 1994).

Old growth is structurally different from other developmental stages not only because there are numerous large, old trees, but also because there are fewer trees per acre (Tyrell and Crow 1994, Schwarz et al. 2001). In some old growth, all size classes of live trees tend to have fewer stems per acre, while in other stands this pattern has not been observed. Although there is large variability by forest type and physical conditions such as slope and soil moisture (that is, different forest types are characterized by different structure), basal area (a measure of the amount of wood (tree biomass) in a stand) tends to be greater in old growth, and stands with hemlock consistently support even greater tree biomass than other types (Dunwiddie 1993, Tyrell and Crow 1994, Whitney 1984, Cogbill 1996, Schwarz et al. 2001). Old-growth conifer forests, such as the spruce forests of New England's montane zone and northernmost lowlands and the fir forests of Newfoundland, have been found to have similar attributes of larger trees, and they additionally have a more ragged canopy formed by greater diversity of tree heights (Cogbill 1996, Thompson et al. 1999). In some other forest types, diversity of tree heights was provided by species that tend to grow taller and emerge above the general canopy, such as white pine, rather than by the presence of different-sized trees of the canopy dominants (Whitney 1984, 1994, Dunwiddie et al. 1996).

Dynamics – How Old Forests Change

Forests change as trees grow and die. Changes happen relatively quickly in young forests that are recovering from moderate or severe human or natural disturbances. Many of us are familiar with succession, the dense growth of tree saplings and blackberries that fills large openings in the forest, and the several decades of very rapid changes that ensue. The early successional trees, such as pin cherry, paper birch and aspen, need high levels of light to germinate and survive, and they have one-third or less the longevity of the older forest denizens. As the early successional trees die, the later successional species, which are able to grow and survive in the shade of a forest canopy, gain dominance. Once the longer-lived, mid- and late-successional trees gain prominence in the canopy, the changes to the species composition and the structure of the forest come more slowly, but the forest continues to change even after 375 years without major disturbance (Tyrell and Crow 1994). Through these changes, old growth gains unique characteristics, such as many canopy gaps, abundant dead wood, and, as discussed below, the development of habitat for numerous species that find resources in the structural diversity of live and dead trees, the deep litter of the forest floor, and the soil.

The principal type of change in older northern hardwood forests is "gap formation." Gaps have been intensively studied in many forests young and old. The pattern of gaps (including their number and size in a forest) is integral to the population processes of trees, shrubs, herbs and animals. Gaps are formed when one or several trees die and thus make space for other trees to grow. Small-gap formation by the death of one or a few trees is the commonest disturbance in old forests (Foster 1988a, Mladenoff et al. 1993, Tyrell and Crow 1994, Dahir and Lorimer 1996, Runkle 1998, Runkle 2000). Because there are larger trees, as well as fewer trees, the gap pattern in old-growth forests differs from that of younger forests. Most old-growth forests have more gaps than stands of younger ages, and the gaps tend to have a larger average size and cover a greater percentage of the forest area. Even though the gaps in old growth are larger, single trees create over three-quarters of gaps in old growth. Also, although larger than natural gaps in younger stands, the gaps are really rather small; average size is about 500 square feet, or 1/100 of an acre, and the larger ones are only approximately 2,000 square feet (Tyrell and Crow 1994, Dahir and Lorimer 1996). In a study of old-growth stands aged 177 to 374 years, it was discovered that the total area of gaps continued to increase with age; that is, the gap structure had not reached equilibrium in the forest even after 374 years without severe disturbance (Tyrell and Crow 1994). Nevertheless, the basal area, tree density (in all size classes) and sapling and seedling density did level off after 275-300 years (Tyrell and Crow 1994, Woods 2000a, Woods 2000b).

The characteristically small size of old-growth gaps is very important with regard to the tree species that colonize gaps, and thus to the continuity of the composition of the tree canopy. Because the great majority of gaps are no greater than 1/100 to 2/100 of an acre, the dominant overstory trees are able to replace themselves in most situations, and in few gaps do species other than the canopy dominants establish. Species that are often thought of as "gap specialists" – yellow birch, white ash, and basswood – appear to much less frequently colonize gaps in old-growth forests; rather, such species apparently need a coalescence of several gaps, a more severe disturbance, or, in the case of yellow birch, uprooting of trees to create areas of bare soil (Nakashizuka 1989, Houle 1992, Dahir and Lorimer 1996, Runkle 1998, Peterson and Pickett 2000). It has thus been observed by resampling plots in old growth 60 years after they were initially sampled, that the abundance of yellow birch declines as northern hardwood forests reach ages over 200 years (Woods 2000a). Since only 6-25% of the gaps in old-growth forests were found to have been created by tip-ups, not much soil is bared, and yellow birch declines as a forest ages (Dahir and Lorimer 1996, Runkle 2000). These dominant natural disturbance patterns differ greatly from the changes that result from human management, and thus the species composition, age- and size-structure, and gap structure differ substantially between old growth and younger, managed forests.

Northern deciduous forests are "slow systems." That phrase has been applied because the dominant trees reside in the canopy for 150 or more years and stand-initiating disturbances occur very infrequently (on the order of 1,000 years or more) (Woods 2000a). Forests of southeastern New England are close enough to the Atlantic Ocean that hurricane disturbance is much more frequent than in northwestern New England (Boose et al. 2001). With regard to disturbance regime, forests in Vermont, western Massachusetts, northern New Hampshire, and northern New York are more similar to those in the Lake States of Michigan and Wisconsin than to those forests adjacent to the south and coastal regions. Northwestern New England was found to have a mean hurricane return time of over 200 years for minor storms that produce scattered blowdowns and small gaps and over 380 years for storms that result in extensive blowdown and large gaps (Boose et al. 2001). Furthermore, many stands may be in landscape positions that are more protected from storm disturbances and may not see severe weather for 1,000 years or more (Lorimer 1977, Foster 1988a, Foster 1988b, Seischab and Orwig 1991, Cogbill 1996, Boose et al. 2001). Forest history analyses of stand-initiating disturbances in northern and western Maine indicated that 55-60% of the northern forest was originally greater than 150 years old, and due to similar forest disturbance patterns, that proportion can be extrapolated across northern New England and New York as well (Cogbill 1996). Thus, over half of the forest that the European settlers saw in the region was old-growth forest.

Although the presettlement forest was comprised of the same tree species that we encounter in the post-disturbance forest, they occurred in substantially different proportions (Siccama 1971, Seischab 1990, 1992, Marks and Gardescu 1992, Cogbill 2000, Cogbill et al. 2002). Beech, spruce, maples (mostly sugar maple) and hemlock were the four dominant trees of northern New England and New York (Cogbill 2000, Cogbill et al. 2002). In the post-logging forests of the region, beech has declined to one-fifth of its presettlement abundance, and there have been substantial declines in spruce and hemlock also (Siccama 1971, Cogbill 2000). Such drastic change in the abundances of dominant species has implications for food chains, cycles of wood and litter decomposition, populations of the organisms involved in decomposition, and resources for numerous animal species. Research involving insects, fungi, and lichens that will be discussed below has highlighted some of these relationships; however, since old-growth remnants are so few and so small, it is difficult to correlate tree composition and abundance changes to other alterations.

Because large, intense disturbances occur only infrequently, the natural northern hardwood and mixed forest landscape of northern New England, New York, and the Lake States was dominated by old, uneven-aged stands, but also included patches of single- or several-aged stands representing different stages of successional development (Frelich and Lorimer 1991). In a comparison of an old-growth landscape and a typical disturbed landscape like those that dominate the eastern forest, it was found that the disturbed landscape had a smaller range of patch sizes, patches with simpler shapes, and more patches (Mladenoff et al. 1993). Whereas the old-growth landscape had maximum interspersion of both forest interior and patches, the disturbed landscape had lower connectivity and greater habitat isolation. In short, disturbed landscape had an artificially elevated diversity of successional forest types at the expense of what naturally would be the common matrix, old-growth forest. In changing the patch pattern in the forest, humans have created many high-contrast edges that are not part of the natural workings of the forest. The high-contrast edges in the natural landscape were most pronounced between upland and wetland natural communities. The successional patches interspersed within the old-growth landscape featured softer edges characterized by a lower contrast in forest structure than was observed in the manipulated forest landscape. Thus, our utilization of the forest has changed habitat proportions, contrast, and juxtapositions at the landscape level, which is a scale of great importance to maintaining populations of wide-ranging and migratory species.

Not only does the pattern of gaps and successional patches differ among old growth and other forest stages, but also the death of trees and distribution of tree death by size class differ. The rate of tree death was four times greater in old-growth forest than in both forests in younger successional stages and forests that were selectively logged 100-170 years ago (Lorimer et al. 2001). The large-tree size classes in old growth are very dynamic, with continuous death as well as recruitment from smaller size classes. About 1% of the trees in an old-growth forest die each year, and for the larger sizes (greater than 20" dbh), up to 3% mortality per year has been measured (Runkle 2000, Lorimer et al. 2001). Despite this rate of death, the percent of the trees accounted for by large stems remains stable or even increases, due to the growth of smaller stems into the large size class. This continual death of trees is integral to the dead-wood component of the forest ecosystem, and, as is discussed in the sections below, dead wood is a part of the forest that is involved in many processes related to soil, nutrients, and wildlife habitat.

Coarse Woody Debris

Dead wood is a feature that differs strongly between old growth and younger forests. It is customary to differentiate between snags, which are standing dead trees, and downed wood; snags and downed wood provide special habitats that cannot develop elsewhere in the forest, and both are very important for the existence of the natural array of habitats necessary to support the full biodiversity of wood-decomposing species in the forest. Also, in New England, one-third to one-half of amphibian and mammal species rely on standing or downed logs for some aspect of their life histories (DeGraff et al. 1992 cited in McGee et al. 1999). Among eastern forests, those that are cooler (northern hardwood, northern hardwood-hemlock) tend to have greater amounts of coarse woody debris than the warmer types that occur at lower latitudes or lower elevations; cooler-climate forests not only have slower decay rates, but also receive higher input of dead wood due to snow and ice-loading (Muller and Liu 1991, Hardt and Swank 1997, McGee et al. 1999).

The natural functioning of the forest depends on the presence of dead wood in large and small size classes and in newly dead to highly decomposed decay categories. The functions and role of woody debris in the forest are very complex, and we still know very little about it in eastern deciduous forest. Nevertheless, it is clear that coarse woody debris is very important to nutrient retention and cycling, as well as species diversity and abundances of insects, fungi, mosses and liverworts, and vertebrates (Harmon et al. 1986). The functional importance of dead wood will become apparent in the discussions of different animal groups, for many species require or preferentially utilize dead wood. The following paragraphs address the characteristics of dead wood in old growth.

Old growth throughout the eastern deciduous forest region generally has two to four times as much coarse woody debris compared to forests logged 100 years ago (Tyrell and Crow 1994, Goodburn and Lorimer 1998, McGee et al. 1999, Spetich et al. 1999, Runkle 2000, Fisk et al. 2002, Fan et al. 2003, Hura and Crow 2004). Snags and downed logs are continually created; natural forest dynamics produce approximately two snags per five acres each year, and nearly 10% of these may fall to the forest floor annually (Runkle 2000). Typically, old-growth eastern deciduous forests feature four to ten snags per acre, which in most studies has been found to be at least twice as many as in either recently managed forests or forests that were logged a century ago but have not seen active management since. Old-growth hemlock-northern hardwood forests have even more snags, as many as 16 per acre (Goodburn and Lorimer 1998). Additionally, the size of dead trees is significantly greater in old-growth forests; younger stages of development tend to have very few snags greater than 20" dbh (Goodburn and Lorimer 1998, McGee et al. 1999, Spetich et al. 1999, Hura and Crow 2004). In old growth in the Adirondacks and the Lake States, large trees constituted 20-30% of all snags, whereas the big trees comprised a mere 0-1% of the snags in younger forest classes (McGee et al. 1999). Similarly, the same study found that large logs accounted for nearly 20% of the downed dead wood in old growth but only 4-8% in younger forests.

Snags and downed logs in the large size classes cannot be created in young northern hardwood forest, for they do not develop until a stand is at least 170 years old and the large, old trees begin to die. The large-diameter dead wood, in addition to its importance in regulating energy flow and nutrient cycling, is important habitat for large-bodied species such as marten, fisher, raccoon, and pileated woodpecker. It is also important for plants and small animals; for instance, soil beneath rotting logs harbored greater nematode density and root biomass than did soil under leaf litter (Ausmus 1977 cited in Harmon et al. 1986), and mice selected logs to travel on more than any other type of substrate in the forest (Barnum et al. 1992). Small-diameter logs decompose faster than large-diameter ones (for any given species), and the diameter-decay relationship along with the more continuous creation of coarse woody debris in old growth contribute to both greater abundance and a more continuous supply of dead-wood habitat features.

Because old-growth forests both receive a continuous supply and have had more time to accumulate dead wood, they also feature a greater diversity of decay classes (Hura and Crow 2004, Tyrell and Crow 1994). The presence of rotting wood at different stages of decay is very important to the diversity of insects, the provision of germination sites for plants (and thus the structure and species composition of the tree and herb layers), and nesting and feeding habitat of birds and other animals. Despite the fact that dead wood always eventually does decompose and become incorporated into soil as organic matter, no leveling off of snag basal area or coarse woody debris volume was observed in the study of old-growth forests aged 177 to 374; rather, both of those measures of dead wood were seen to increase linearly with stand age (Tyrell and Crow 1994). Density of snags did, however, show a leveling off at age 275 to 300.

Cavity Trees

Just as coarse woody debris is more abundant in old growth, so are tree cavities, holes in dead or live trees. Cavities have received a great deal of attention from wildlife managers, because many bird and mammal species require them for shelter and/or breeding habitat. Old-growth forests in the Midwest were found to have five times more cavity trees per acre than younger forests, and nearly one-third of all trees over 12" dbh in old growth had cavities (Fan et al. 2003). Similarly, in the Lake States old-growth forest had 30% more cavity trees than uneven-age forest managed for timber and wildlife, and larger trees were more likely to have cavities (Goodburn and Lorimer 1998). In that study, the managed stands had more "wildlife trees" retained per acre than was even called for in the state forestry guidelines.

Not all cavity trees are dead. In fact, both of the studies cited above found that a very large percentage (as much as 85%) of cavities were in live trees, pointing out that live trees perform a function that is often thought of as being most connected to snags. Both live and dead large trees play important roles that scientists are just beginning to document and understand. Further discussion of cavities continues in the sections below that concern different animal groups.

Forest Herbs and Seed Banks

Eastern old growth characteristically has more herb species and greater herb cover than previously logged stands (Duffy and Meier 1992, Meier et al. 1996). In Appalachian Mountain forests, herb species diversity was nearly double in old growth and cover was 2.5 times greater compared with stands logged 50-85 years prior. Among second-growth forests, only moist (mesic) areas had extensive herb cover, another indication that different forest types within a landscape respond differently to human manipulations. A study of western trillium in the Pacific Northwest provides some understanding of the processes that may be affecting forest herbs when logging occurs (Jules 1998, Jules and Rathcke 1999). Even after 30 years, there was no recruitment of trillium into heavily logged areas, and forest edges adjacent to the logged areas also experienced almost no recruitment. In unlogged forest interiors, trillium reproduction was at higher levels. In addition to the changes to the forest-floor moisture and temperature regime, changes in rodent communities that accompany logging may be detrimental to the reproduction of trillium.

In old-growth forest in Michigan, herbaceous species responded differently according to the density of saplings in study areas, and it appeared that competition with sugar maple saplings strongly determined patterns in the herb layer (Miller et al. 2002). Sugar maple has increased substantially in the post-logging northern hardwood forests, and this may have altered the herb community for centuries to come. In addition to sapling density, the distribution of both coarse woody debris and pits and mounds on the forest floor were important for maintaining plant diversity in the old-growth forest. From the canopy to the forest floor, the disturbance pattern and the regeneration dynamics of trees has an immense impact on all forest species and their population dynamics. The living and dead large trees, the creation of pits and mounds, the abundance of small openings and scattering of large ones, and the amount and continuous input of coarse woody debris all differ between old growth and younger forests, and these forest characteristics and processes are strong factors in determining the population levels of the smaller plants (Gilliam and Roberts 2003).

Once seeds fall to the ground, their fate is little noticed, but in yet another element of the forest ecosystem, old growth differs from secondary forests. Seed banks (buried seed supply) in old-growth stands, including a deciduous forest in Quebec, frequently feature more species than are found in seed banks in younger forests (Pickett, and McDonnell 1989, Leckie et al. 2000). Additionally, beech-birch-maple forest over 200 years old had greater abundance of seeds in the seed bank compared with 95-year-old forest of that type (Graber and Thompson 1978). Differences in canopy composition (deciduous vs. coniferous), soil type, and organic-matter decomposition rates appear to have strong control on seed banks, and those factors must be considered when comparing seed banks among forest age classes (Pickett and McDonnell 1989, Leckie et al. 2000). The available research shows that old growth characteristically has greater seed diversity and abundance than younger stands.

Numerous studies have documented the importance of the seed bank to the process of gap revegetation (Oosting and Humphreys 1940 and Marquis 1975 both cited in Pickett and McDonnell 1989; Mladenoff 1985), and the amount of gaps and their importance to the animal species of old-growth forests is a theme that is continually re-iterated in old-growth forest research. Work in Quebec and Japan has shown that many species in old growth do bank their seeds, and old-growth seed banks more closely resemble the aboveground native vegetation than has typically been found in forests after human disturbance (Nakagoshi 1984, Nakagoshi 1985, Leckie et al. 2000). Additionally, it has consistently been found that the spring wildflowers – familiar species such as trillium, spring beauties, hepatica, and Dutchman's breeches, whose colorful abundance paints the forest floor prior to the leaf flush of the trees – are not represented in the seed bank. The spring wildflowers depend on propagation from the current year's seeds as well as vegetative reproduction from underground parts (Leckie et al. 2000). Although these few studies have shown that old-growth seed banks differ from those of younger forests, not enough is known to be able to explain the significance of seed-bank differences to the composition and function of the forest ecosystem.

Lichens, Mosses, and Fungi

Lichens are an often overlooked, but very common component of forests. They are important in nutrient cycling processes, for they take-up nitrogen and other elements from the atmosphere, and they send them downward in the forest as litter and dissolved in water (Esseen et al. 1996). Lichens also serve as food and shelter for many mammal, bird, and invertebrate species. Research in North America and in Europe has shown that the community of epiphytic lichens (those that grow on tree trunks and branches) in old-growth forests differs significantly from that in more disturbed forests (Stevenson 1988, Neitlich 1993 both cited in Esseen et al. 1996; Rose 1992, Lesica et al. 1991, Esseen et al. 1996). Coniferous forests have seen the most documentation of old-growth lichen communities. In both Montana's fir forests and Europe's spruce forests, lichens were two to six times more abundant in old growth (Lesica et al. 1991, Esseen et al. 1996). Species of broad, foliose as well as pendulous, fruticose lichens have been observed to require late-successional to old-growth conditions to become abundant. The more equable climate and the longer time available for lichen propagules to colonize tree branches and trunks were implicated as features related to the much greater abundance of some lichen species in the old-growth and late-successional stands.

Mosses and liverworts, together known as bryophytes, also are different in old growth versus managed forests. Up to 50% of the species of bryophytes in old growth did not occur in the younger forests (Lesica et al. 1991, Vellak and Paal 1999). Liverworts may be more sensitive to loss of old growth than mosses; 30% of the bryophyte species in Estonian old-growth forest were liverworts, whereas in the managed forest liverworts accounted for only 17% (Vellak and Paal 1999). Of the 20 species that grew only in old growth, nine lived on decaying wood and three on the trunks of large trees; thus, once again we see the importance to other species of the coarse woody debris and large-diameter trees characteristic of old growth.

Fungi also have been found to be more diverse and more abundant in old-growth forest compared to managed forests (Smith et al. 2002). In the Pacific Northwest, 20% of the fungus species and 8% of the genera were unique to old growth, and five of the genera contributed a higher proportion of the fungal biomass in old-growth forest. The researchers concluded that fungus species composition and abundance were altered due to forest management, and species or genera unique to a certain age class were much more likely to be restricted to the old-growth stands. Fungus species that produce spores below ground are an important part of the forest ecosystem, for they have functions in tree regeneration and growth and are a food resource also; these are discussed below in conjunction with the small mammals that disperse their spores. In Finland, researchers discovered that an old-growth forest specialist bracket fungus, Fornitopsis rosea, was the base of a food chain that supported many old-growth specialist insects; fragmentation of the forest has truncated that food chain and led to loss of species in isolated old-growth fragments (Komonen et al. 2000). Such relationships among old-growth specialist species in groups that are not well known, such as invertebrates, fungi, bacteria, and lichens, may persist in tiny old-growth patches in the East, or the interrelationships and the old-growth specialist species may have been lost entirely.

Plant Genetics

Genetic diversity has eroded worldwide as diverse natural vegetation is homogenized into fields or plantations of one or several species. How much genetic diversity was lost in the clearing of the eastern forests? That question can never be answered satisfactorily, but research from old-growth white pine forests that were recently logged clearly indicates that genetic erosion had occurred in the harvested populations (Buchert et al. 1997). Seventy-five percent of the standing trees were harvested from the studied stands, and that resulted in a 25% reduction of the genetic diversity. Of great concern is that 80% of the alleles (alternative forms of a gene) that were rare in the populations were lost, and 40% of those that occurred infrequently were also lost. Thus, the genetic potential of each old-growth pine stand was reduced by approximately 50%, and the ability of pine populations to respond to changing environmental conditions may have been substantially compromised. Clearly, the loss of so much old growth in the 18th and 19th centuries diminished the gene pool of not only the dominant tree species, but also of all other forest species, whose populations were greatly reduced in that time period as well. It will require numerous tree generations (150 years or more) for those species to develop mutations to replenish the genetic diversity that natural, undisturbed forests contain.

Animals in the Old-Growth Ecosystem

Birds

Old-growth forest provides habitat structures and a landscape pattern that favors greater abundances of some bird species. No birds of the eastern deciduous forest are known to require old growth, but it is suspected that the changes resulting from forest clearing and the down-aging of the eastern forests aided, hastened, or perhaps was fully responsible for the extinction of the passenger pigeon (Haney and Schaadt 1996, Askins 2000). Old growth provided larger trees, a more open understory, and a greater volume of nuts (beech nuts in northern New England and acorns to the south) than do younger stands. John James Audubon described the passenger pigeon's habitat as "forests where the trees were of great magnitude, and where there was little underwood" (from Bent 1932 cited in Haney and Schaadt 1996). The forest structure differences discussed above speak to the larger trees and the lower density of trees in both the overstory and the understory. As mentioned above, presettlement-forest research has shown the great decline in beech throughout the Northeast, so, although we will never be able to prove the relationship, it is safe to assume that the widespread changes to the original old-growth forest landscape contributed strongly to the extinction of this one bird species. It has not gone unnoticed that the over-harvesting of the passenger pigeon also played a role in the species demise. In the southeastern U.S., the massive landscape changes and removal of old-growth forest have been principal factors in the near extinction of the ivory-billed and red-cockaded woodpeckers.

Although no direct link has been made between a bird species and the requirement of northeastern old-growth forest habitat for its survival, old-growth forests do provide unique characteristics that benefit numerous species in the avian communities. Species abundances and ecosystem function are altered in younger forests, with subsequent impacts to bird communities. In a study of old-growth forest in Pennsylvania, compared with other forests throughout the local area, the state, and the entire Northeast, one-third of all breeding birds found in old growth were either rare or uncommon over broader forested landscapes (Haney 1999). Sixteen species were more likely to occur in old growth than in the broader region, and 15 species were "old-growth associates," whose abundances were much greater in old-growth forest. The list includes blackburnian warblers (45 times more abundant in old-growth), magnolia warblers (40 times more abundant), Swainson's thrush (20 times more abundant), solitary vireo (8 times more abundant), brown creeper (4 times more abundant), and black-throated green warbler (3 times more abundant) (Haney and Schaadt 1996). Barred owls were in or within 330 feet of every old-growth fragment surveyed; owl reproduction was associated with lower understory densities, higher snag densities, greater basal area of large snags, and a greater likelihood of hemlock snags (all features of old growth in contrast to younger stages) (Haney 1997). Certain birds were also found to use old growth preferentially in the winter, and the winter bird community in Pennsylvania old growth was statistically distinct from that of other age classes. Red-breasted nuthatch, golden-crowned kinglet, and brown creeper were consistently more abundant in old growth versus younger forest in winter. Similar results were detected in old-growth balsam fir forests in Newfoundland (Thompson et al 1999), where black-backed woodpecker and gray-cheeked thrush were associated only with old growth, and ruby-crowned kinglet, dark-eyed junco, brown creeper, olive-sided flycatcher, winter wren and black and white warbler were strongly associated with old growth.

In addition to those birds that show greater abundances in old-growth forest are those that can utilize old growth but are not typically found in younger, upland forests. Winter wren and red-shouldered hawk are both considered birds that favor riparian, ravine, or wetland forests; these species are, however, also found in upland forests if they are old growth (Haney and Schaadt 1996). The structural features of old-growth forest, especially structural and dead-wood diversity, provide the habitat needs that in younger forests those species find only in wetter parts of the landscape. Additionally, the naturally greater abundance of cavities in old growth provides for more habitat for cavity nesters such as nuthatches, barred owl, chimney swifts, woodpeckers, and common mergansers.

Woodpeckers are a group of birds that are known to depend on snags and cavity trees; thus one might suspect that woodpecker populations are limited by the documented lack of cavities in younger forest. A study in western New York, however, found that woodpecker populations were not limited by the availability of cavity trees, but there were other, undetected, forest characteristics that appeared to have been limiting populations (Welsh and Capen 1992). What is it about old-growth forest that allows for greater abundances of some species? The overall structural complexity and the tree composition of old-growth forest create a different environment for forest birds. In many places in the Northeast and Lake States, hemlock becomes more abundant in old growth, and thus species that prefer conifers, such as saw-whet owls, red-breasted nuthatch, golden-crowned kinglet, Swainson's and hermit thrushes, and pine siskins, find better habitat. Additionally, the pattern of numerous gaps provides structural complexity that midstory nesters such as magnolia and black-throated blue warblers require (Haney and Schaadt 1996). Further evidence for the importance of the numerous small gaps in old-growth forest comes from a well-studied tract in Poland; there, the number of bird species and the number of individuals were both significantly higher in gap areas, but, in a somewhat counterintuitive result, very few species showed an actual preference for either gap or non-gap habitats (Fuller 2000). The study indicates that the pattern of numerous small gaps is important to many birds, and the managed, younger forests have a very different gap mosaic than what develops naturally.

Emergent white pines, tall trees that extend above the canopy, are found in many old-growth forest types, and these provide habitat for pine warbler, for instance, a species that would not find suitable habitat in a younger stand which lacked the old-growth structural complexity (Haney and Schaadt 1996). Similarly, emergent conifers provide special habitats that are utilized by hawks and owls for perching and by great blue herons for their nesting colonies (author's observation). For overwintering birds, old growth also provides a different environment; the tall canopy of large crowns moderates the climate and the winds inside the forest; the abundance of hemlock or spruce provides a larger cone crop; the great age and size of trees provide for different bark textures that are of importance to trunk-bark foraging species; and the numerous snags and dead limbs provide a more continuous supply of winter forage (Haney and Schaadt 1996).

Northern goshawk is frequently mentioned in association with later successional forests and old growth. In fact, goshawks do preferentially select areas with forest structure that is characteristic of old growth (Speiser and Bosakowski 1987, Daw and DeStefano 2001). In the eastern forest, goshawks had significantly more nests in older and old-growth hemlock-hardwood forests than in any other stand types. Although hemlock dominance and density were significantly greater at nest sites than at random locations in the studied forests, nest trees were most often deciduous trees, especially beech and black birch. We do not know how goshawk densities and nesting preferences differed prior to the clearing and down-aging of the spruce-hardwood forests of northern New England, but if their preference for mixed hemlock-hardwood forests can be extrapolated to mixed spruce-hardwood forests, goshawk nesting habitat was likely much more abundant in the presettlement, old-growth northern forest.

Pileated woodpecker is another species that has an association with forest structures known to be more abundant in old growth – large live trees greater than 18" dbh and large dead or dying trees (DeGraaf and Yamasaki 2001). In the Pacific Northwest, pileated woodpeckers did not use snags that were retained in heavily logged areas prior to the re-establishment of late successional conditions (Aubry and Raley 2002). Pileated woodpeckers excavate nesting and roosting cavities in recently dead snags and in decadent live trees, and they furthermore require numerous large trees in one area. Over a three-year period, one tracked individual used 29 different roost trees; thus the significance of the number and continual supply of new snags and decadent large trees characteristic of eastern old growth is not trivial to this species. Pileated woodpeckers have returned to many forested areas in New England since reforestation commenced after the land-clearing and heavy lumbering of the 18th and 19th centuries; nevertheless, based on data about forest structure of live and dead trees, old growth would appear to be where habitat conditions are optimal. Moreover, pileated woodpeckers may play a very special role in the forest ecosystem, a role that has been termed “keystone species.” Keystone species are integral to the function of ecosystems because they perform special, and often specialized, functions that other species do not perform. In the case of pileated woodpeckers, their excavation of large cavities is a process that influences numerous other species and ecological cycles (Aubry and Raley 2002). Other species such as bats, marten, fisher, flying squirrels, wood duck, and various owls establish den and nest sites in the cavities initially created by these large woodpeckers. Also, numerous other species forage in the cavities; the cavities accelerate decomposition and nutrient cycling; and pileated woodpecker feeding mediates insect outbreaks. Thus, these birds have far-reaching influences on the function of forest ecosystems, and the diminishment of large-tree habitat structures and alteration of dead-wood dynamics in younger, managed forests that has contributed to a deterioration of their habitat, cascades to numerous other species and interactions.

Although we now have no living species whose existence has been tied to the presence of old growth in the eastern deciduous forest region, we do know that for some bird species, populations are greater in winter and/or summer in old growth. We also know that a number of the forest bird species that are in greatest decline in the Northeast are neotropical migrants that spend summers in our forests and winters in the Caribbean or South or Central America (Hagan and Johnston 1992), and that neotropical migrants nest in greater density in old-growth forest than in younger, managed forests (Haney and Schaadt 1996).

Mammals

Large mammals are an obvious and charismatic part of the forest ecosystem. Within historic times there have been large population shifts in both herbivores and carnivores (Whitney 1994); the most notable for old growth are perhaps the regional extinction of two top-level carnivores, eastern timber wolf and panther, and the currently high densities of white-tailed deer in many eastern forest landscapes. Both of these shifts have altered ecosystem processes and interactions, and while scientists have documented the detrimental effects that elevated deer herbivory has had on old growth tree and herb vegetation in Pennsylvania (Whitney 1984, Rooney and Dress 1987), it is harder to document the cascading effects from carnivore extinction.

More frequently, small mammals have been studied in old growth. From ground-dwelling shrews to arboreal squirrels to flying bats, small mammals abound in forests and they perform diverse functional roles. A short list of those functions includes prey supply for carnivorous birds, mammals, and reptiles; predators of insects, other invertebrates, and bird eggs; consumers of lichen, fungi, and plants and their fruits and seeds; and disseminators of seeds and spores. Many small mammals in North America are generalists that are not closely associated with rare habitat features; nevertheless, forest structure and composition are closely associated with the diversity and abundances of small mammals (Carey and Johnson 1995). Coarse woody debris, understory and herb composition and abundance, and soil organic layers are all of great importance to populations of small mammals (Carey and Johnson 1995, DeGraaf and Yamasaki 2001).

Southern red-backed vole is a rodent common throughout many forest types in New England (DeGraaf and Yamasaki 2001). It has not been studied in old-growth forests in our region, but studies from the Pacific Northwest show significant differences in red-backed vole abundances and breeding populations among large tracts of old growth, old-growth corridors (with minimum 0.6 miles width) within second-growth forest, and second growth (Pereault and Lomolino 2000). More males and females in breeding condition were observed in the continuous old growth than in the other types, and abundance of the voles was higher in the old-growth corridors than in the surrounding second growth. The impacts of forest age and old-growth forest shape and size operated at a population level; that is, not only were numbers impacted, but also breeding demography was impacted by the changes associated with forest harvesting. Old-growth forest structures, such as coarse woody debris and complex vegetation height structure, were important characteristics associated with these differences, as were the width of old-growth remnants and the adjacency of large old-growth tracts to the narrower old-growth remnants. In addition to these effects, population densities of three of the six small mammal species present were greater in and near old growth, as well as in wider old-growth corridors. A similar study found that there were 1 1/2 times more individuals and more biomass in old-growth forest than in managed forests (Carey and Johnson 1995). Forest features that were associated with the larger populations in old growth were coarse woody debris, plant composition, shrub and herb cover and abundance, and soil organic layers. All of these features have been shown to differ among old growth and younger forests in the East.

Northern flying squirrel is part of an interesting relationship that includes truffles, mushrooms that produces spores beneath the ground (Cotton and Parker 2000, Waters et al. 2000, Pyare and Longland 2001). Numerous species of trees, especially conifers, establish better and grow more productively when their roots are in association with mycorrhizal fungi, a group that largely produces spores beneath the ground. Studies in western North America have elucidated a link between northern flying squirrel and not only these ever-important mycorrhizal fungi but also lichens. The flying squirrels consume spores and other propagules and disperse them throughout the forest. Red squirrel may perform some of the same functions, and it has even been seen that northern flying squirrels steal fungi from red squirrel caches (Mowrey and Zasada 1984 cited in Cotton and Parker 2000). Neither deer mice nor chipmunks performed these spore dispersal functions, and some of the spores found in the flying squirrel feces were of fungi that were rare (Cotton and Parker 2000). Furthermore, disturbance was seen to change the truffle community in the forests; in one study, four of the ten most common species were significantly more common in old growth than in either old growth selectively logged six years prior or in 80-100-year-old forest (Waters et al. 2000). Although there were differences in the frequencies of truffle species between the old growth and the regenerated forests, the researchers did not find any difference in biomass or species numbers between old growth and the 100-year-old forest. Thus, the changes wrought by forest management to truffle communities are species specific – some species are lost from the managed forest while others appear. Furthermore, old-growth stands had greater abundance of northern flying squirrels than recently selectively logged forest or 100-year old forest (Waters et al. 2000). Northern flying squirrel is another species that dens and nests in tree cavities; and old-growth forest includes more of these important shelter habitats. Old growth may also feature more even distribution and greater biomass of truffles (Mills 1995). Similar to pileated woodpeckers, northern flying squirrels utilize numerous nest trees per season, five or six on average (Cotton and Parker 2000). In both eastern and western North America, northern flying squirrels preferentially selected trees with greater diameter, age, and height for nesting; the squirrels also almost always chose live trees with intact crowns, very little or no missing bark, and relatively sound wood in the tree's bole (Gerrow 1996, Cotton and Parker 2000). Again, it is seen that "wildlife trees" are not dead or nearly dead decaying snags, but are vigorous trees that are perhaps chosen because they afford greater protection from weather and predators (Carey et al. 1997). The complexity of the forest ecosystem and the complex impacts of human disturbance of old-growth forest are exemplified by the flying squirrel-truffle relationship.

American marten, one of the larger members of the weasel family, is another species that shows a strong affinity for old-growth forest structures. Marten require large logs or trees for their dens (Wynne and Sherburne 1984, Chapin et al. 1997 both cited in DeGraaf and Yamasaki 2001). Marten population levels have been correlated to high density of large diameter snags (Spencer et al. 1983, Lofroth 1993, Drew 1995 all cited in Hargis et al. 1999), and they shy away from even low levels of forest fragmentation (Chapin and Harrison 1998 cited in Hargis et al. 1999, Hargis et al. 1999). Like many other species discussed, marten utilize numerous den trees in any given year (Wynne and Sherburne 1984 cited in DeGraaf and Yamasaki 2001). The Eurasian pine marten in Sweden was found to occur in old growth in abundances two to three times greater than in the surrounding managed forests (Bjärvall et al. 1977 cited in Hargis et al. 1999). Marten use the structural features of older forests to avoid predators, gain access to prey in winter, and acquire heating advantages while resting in winter (Hargis et al. 1999; and Steventon and Major 1982, Corn and Raphael 1992, Sherburne and Bissonette 1994, Chapin et al. 1997, and Gilbert et al. 1997 all cited in DeGraaf and Yamasaki 2001). Thus, although marten are able to survive in habitats other than old-growth forest, managed forests are unlikely to provide the abundance or diversity of forest structures that make for good marten habitat. Patchily logged forest landscapes may be able to maintain marten populations, but in those places the animal's home ranges are limited by the amount, size and configuration of remnant old-growth patches (Chapin et al. 1997 cited in DeGraaf and Yamasaki 2001).

Bats in Ontario and the Pacific Northwest have also been seen to have larger populations in old growth (Humes et al. 1999, Jung et al. 1999). In Ontario, Myotis species were three to five times more common in old growth than in younger forest, and silver-haired and hoary bats were also more common in old growth (Jung et al. 1999). Of the entire bat fauna in the forests, only the red bat was less common in old growth; that species prefers edge habitats (Constantine 1966 cited in DeGraaf and Yamasaki 2001) and selectively logged forests (Jung et al. 1999). Once again, forest structures characteristic of old growth – density of large trees and large snags, high basal area, greater canopy closure, and small mean gap size – were associated with the larger animal populations.

Amphibians and Reptiles

Salamanders and frogs are the most abundant vertebrates in many temperate forest ecosystems. As important predators and prey they are of great significance to ecosystem function. Old-growth forest, with its abundant coarse woody debris, deep litter layers, equable forest-floor temperature and moisture, and dense herb layers, provides habitat where salamanders can reach their highest population densities, and in some places greater species diversity as well (Welsh 1990, Petranka et al. 1993, Petranka et al. 1994, deMaynadier and Hunter 1998). Conversely, bare soil, high light levels, and grass, all of which are associated with logging, were negatively associated with salamander and frog abundance in New England forests (deMaynadier and Hunter 1998). Of the New England amphibian fauna, red-backed, spotted and blue-spotted salamanders, as well as wood frog, were highly sensitive to forest harvesting.

Not only are various species of salamanders highly sensitive to forest harvesting, but also their populations recover slowly after logging. Salamanders disperse very slowly and have longer generation times than most other small vertebrates (e.g., rodents). They are also territorial and have strong fidelity to small home ranges. Therefore, individuals that need to find new homes after logging cannot easily move to an adjacent patch of uncut forest and find unoccupied territory. What do displaced salamanders do when conditions in their existing habitat become unsuitable for their survival? They likely either go underground where they starve for lack of food, or they move to new areas but typically cannot establish because other salamanders have territorial control (Petranka et al. 1994). Because of such life-history characteristics, some salamander species apparently require 120 or more years to recover from clearcutting. A 70% decline in salamander abundance has been estimated for the southern Appalachian Mountains, where the logging history was not very different from in the Northeast. Many of the eastern forests, therefore, may not yet have regained natural population levels that existed in old-growth. The effects of such a drastic decrease in one of the most abundant forest vertebrates can clearly ripple up and down the food chain.

Insects and Other Invertebrates

Insects and arthropods perform many ecological functions including pollination, decomposition, and soil mixing and aeration; they also serve as predators, prey, and parasites, and some species are important in controlling outbreaks of defoliating insects. Despite their great species and functional diversity, invertebrates are the least known group of animals. There are several studies, however, in both boreal and northeastern deciduous forests, that show how parts of the insect and arthropod fauna differ significantly between old growth and younger forests.

Beetle studies in New Hampshire comparing old growth with forest selectively harvested 40 years past is clear evidence that old-growth eastern deciduous forest contains both greater species diversity and a greater abundance of many species (Chandler 1987, Chandler 1991, Chandler and Peck 1992). Pselaphidae beetle communities in old growth had 50% more species than in previously harvested forest, and those species associated with deciduous leaf litter or found beneath bark were more abundant in old growth. In other groups of beetles, slime-mold feeders were twice as abundant in old growth, and six of 11 beetle species that feed on fungus under bark in the initial stages of wood decay were twice as abundant in old growth, while the remaining five species were of equal abundance in the two age classes. In the middle stages of wood decay, beetles that feed on exposed fungal sporing bodies are present; among this group six of 21 species were twice as abundant in old growth and the remaining 15 species were equally abundant. Similarly, six of 20 species present beetles in the final stages of wood decay were twice as abundant in old growth, but the second growth did contain seven species that were not found in old growth. Finally, Leiodidae beetles were found to be three times more abundant in old growth, and many of the species that were represented in low numbers in second growth were abundant in old growth. Similar results from a European study found that beetles that feed on rotting wood were strongly affected by alterations in coarse woody debris, decomposition processes, fungus populations, and microclimate (Martikainen et al. 2000). Seventy-eight percent of wood-feeding beetle species were more abundant in European old-growth spruce forest compared with both mature, managed forests, and overmature forest (containing some old-growth attributes but having a history of management). Because small species that are weak fliers and depend on humid conditions apparently have much less ability to recolonize stands after disturbance, the distance to old-growth source patches may be extremely important (Chandler 1987, Chandler and Peck 1992). Studies in other forest ecosystems in Canada, Europe, Japan and Australia have found that a number of beetle, fungus gnat, butterfly and other invertebrate species are old-growth specialists (Spence et al. 1996, Spence et al. 1997, Niemelä 1997, Martikainen et al. 2000, Grove 2002, Maeto et al. 2002).

Alterations in insect communities are strong indicators of changes in ecological processes in a forest, and as with flying squirrels and mycorrhizal fungi, some species associations have been found to be of great importance. Scandinavian scientists have discovered beetle species that specialize on dead wood decayed by fungus species that are only found in old growth (Niemelä 1997). Food-web effects that involve coarse woody debris and fungi are thus again seen to be far-reaching.

Old-growth forests provide habitat that is not impacted by dense road networks and soil compaction. In the Pacific Northwest, compacted soils were seen to have up to two times more soil bacteria than other areas and a concomitant eight-fold increase in bacteria-feeding nematodes (Moldenke et al. 2000). The species composition of the arthropod community thus shifted from one of 78% fruit-feeding mites to one with a very large component of bacteria feeders and nematode predators. How this impacts nutrient cycling or species such as amphibians, birds, and small mammals that feed on the soil-dwelling invertebrates is unknown, but the invertebrate research indicates that forest harvesting leads to a shift not only in species composition and abundance, but also in ecosystem function.

Soils and Nutrients

Forest health is intimately linked to soils and processes that occur in soils. The effects of acid precipitation and the ability of trees to resist weather events and insect and pest infestations have been shown to involve interrelationships between plant physiology and soil processes (Adams et al. 2000, Bailey et al. 2004). Since soil properties result from long-term interactions among soil-dwelling organisms, geologic deposits, vegetation, hydrology and climate, changes to any one of these impacts biochemical processes in the soil, which then has effects on the animals, plants, and other living organisms (Boyle 2000). As many as 40,000 kinds of microbes exist in a teaspoon of forest soil (Moldenke et al. 2000, Richter 2000) and changes to vegetation, such as removing biomass and altering composition by harvesting species of trees means that the diverse populations of millipedes, mites, springtails, bacteria, actinomycetes, fungi, protozoans, and worms that have evolved in forest soils are confronted with new diets that differ in composition and timing from that in the old-growth forest (Boyle 2000). For the soil-dwelling organisms, changes from forest harvesting may be more drastic than evolutionary changes, and the impacts to characteristics such as the productive capacity of the forest may not be seen for many decades.

Harvesting trees removes nutrients from the forest and often increases nutrient leaching from the soil; it can also lead to short-term acidification of soil, which allows aluminum to replace nutrient ions such as calcium and magnesium. Soil acidification and the resultant changes in aluminum, calcium, and magnesium have been implicated in tree declines (Vogelmann et al. 1985, Likens et al. 1998, Markewitz et al. 1998, McLaughlin and Wimmer 1999, Adams et al. 2000). Forest harvesting systems also frequently create many large patches and high-contrast edges where decomposition, nitrogen release, soil moisture and temperature, and patterns of fungal sporing are altered (Edmonds et al. 2000). The effects of different harvesting systems are apparently complicated, and, surprisingly, it has been seen that harvesting systems that remove single trees and do not create hard edges can remove even more nutrients from a forest than more "intensive" cuts that produce unnatural edge and opening patterns (Adams et al. 2000). The intricacies and cascading effects of such changes to the baseline soil properties found in old-growth forests are not well understood, and while studying soil nutrients and organisms may provide specific information, it is important to reiterate that the full extent of the alterations may not be more widely seen in the forest ecosystem for several generations.

Nitrogen, which is often a limiting nutrient in forest ecosystems, behaved differently in old growth versus second-growth forest stands harvested just once in the early 20th century; in short, old growth had greater storage of nitrogen (Fisk et al. 2002). Microbial action in old growth allowed for more effective immobilization of nitrogen, and on average old growth had one-third less leaching loss of nitrogen. Old growth's greater nitrogen pools were primarily due to coarse woody debris, in which three times more nitrogen was stored.

Complex interactions can result from alterations to natural soil properties created both by forest harvesting and by atmospheric pollution. An example is the link between declining nesting success of the great tit and soil acidification (Graveland et al. 1994 cited in Adams et al. 2000, Graveland and Van Gijzen 1994). Thin, weak eggshells were traced to calcium deficiency in the birds' diet, which was linked to a decrease in forest snail populations; the snail decrease was a result of elevated calcium leaching. Undoubtedly, many such interactions are occurring as a result of the changes to soil biochemistry promulgated by both timber harvest and atmospheric pollutants; some soil-dwelling organisms, such as salamanders and snails are very sensitive to soil chemistry. Stories such as that of the great tit or alterations to mycorrhizal fungi life cycles (Edmonds et al. 2000) only scratch the surface. We have yet to discover how effects of soil changes can be tracked all the way up the food chain, for example, to reduced insect predation by birds and altered plant-insect relationships.

Conclusion

Old-growth forests covered nearly two-thirds of the northern New England landscape prior to European settlement. Those forests were characterized by a tree species composition and a structure of live and dead trees that differed significantly from the second-growth forests that now occupy 99.6% of the forested landscape in the Northeast. Concerning live trees, there are differences in size, number of large trees, amount of wood, and proportions of species. The differences with regard to dead trees are perhaps even more significant and far-reaching in the forest ecosystem.

Old-growth forests, in contrast to second growth, contain many times more coarse woody debris, and it is continually created at a far faster and more even rate. Also, in old growth snags are larger and more numerous, and downed wood exists in much greater volume and in a greater diversity of species and decay classes. Coarse woody debris is associated with many of the other differences between old growth and second growth; its abundance, distribution, decay status, and composition affect populations and reproduction of trees, herbs, mosses and liverworts, fungi, mammals, birds, amphibians, insects, arthropods, and nematodes. Impacts also extend to nutrient cycling and storage and to soil properties and processes.

Species from all major groups of animals and plants occur in different compositions and abundances in old growth. Species of insects, fungi, and lichen are known to be restricted to or occur in much greater abundance in old-growth temperate deciduous or mixed forests. Species of small and medium mammals, including carnivores, herbivores and insectivores, occur in greater abundances in old growth. A number of bird species show a preference for nesting in old growth, and thus old growth sustains larger breeding populations and is likely more productive for those species. Some of the same and other bird species prefer old growth for wintering habitat. Old-growth forest sustains larger populations and in some places greater species diversity of salamanders and frogs. Also, old growth maintains a more equable temperature and humidity on the forest floor and in the soil, which is important to the reproduction and dispersal of many organisms and to decomposition processes. The fact that old growth supports many species in greater abundances and with larger breeding populations is important to the landscape as a whole, for old growth can thus likely function as extremely productive source areas (Pulliam 1988, Donovan et al. 1995) for numerous species. Without source areas, especially in the face of down-aging of the forests, many species may see population declines, and their presence, abundance, and functional importance in other forests would be affected.

Pattern differences, as well as population differences, are important. Old-growth landscapes, the landscape pattern in which the forest species evolved in recent millennia, differ from managed landscapes in patch sizes, shapes and juxtapositions. These patterns developed from a regime of disturbance dynamics dominated by many very small-scale wind, ice, and tree-death disturbances. Severe, large-scale, stand-initiating disturbances in northern New England and New York occur only every 1,000 or more years. Thus, on most parts of the landscape, in the absence of human manipulations, the forest has hundreds of years to develop the structure, species diversity, population abundances, and myriad ecological interactions that are characteristic of old growth.

Allowing old-growth forest ecosystems to redevelop on landscapes in the East is an important management strategy, with a solid grounding in the many ecological studies that indicate how different an ecosystem old growth truly is compared with the managed forests that have replaced old growth throughout the region. The first steps toward wise stewardship and conservation of all of the native biodiversity of the landscape should recognize that old growth is in fact a hugely diminished part of the natural diversity of life in Eastern North America, and acknowledge that old growth ecosystems in all their complexity of species, structures, and interrelationships should be better represented among the various forest types in New England.

Literature Cited

Abrams, M. D., S. van de Gevel, R. C. Dodson, and C. A. Copenheaver. 2000. The dendroecology and climatic impacts for old-growth white pine and hemlock on the extreme slopes of the Berkshire Hills, Massachusetts, U.S.A. Canadian Journal of Botany 78:851-861.

Adams, M. B., J. A. Burger, A. B. Jenkins, and L. Zelazny. 2000. Impact of harvesting and atmospheric pollution on nutrient depletion of eastern US hardwood forests. Forest Ecology and Management 138:301-319.

Askins, R. A. 2000. Restoring North America's Birds: Lessons from Landscape Ecology. Yale University Press, New Haven.

Aubry, K. B., and C. M. Raley. 2002. The pileated woodpecker as a keystone habitat modifier in the Pacific Northwest. Pages 257-274 in Proceedings of the symposium on the ecology and management of dead wood in western forests, Reno, Nevada, November 2-4, 1999. GTR PSW-181. USDA-Forest Service, Pacific Southwest Research Station, Albany, California.

Ausmus, B. S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. Pages 180-192 in U. Lohm, and T. Persson, editors. Soil Organisms as Components of Ecosystems. Ecological Bulletin 25. Swedish Natural Science Research Council, Stockholm, Sweden.

Bailey, S. W., R. P. Long, and R. A. Hallett. 2004. Influence of edaphic factors on sugar maple nutrition and health on the Alleghany Plateau. Soil Science Society of America Journal 68:243-252.

Barnes, B. V. 1989. Old-growth forest of the northern Lake States: a landscape ecosystem perspective. Natural Areas Journal 9:45-57.

Barnum, S. A., C. J. Manville, J. R. Tester, and W. J. Carmen. 1992. Path selection by Peromyscus leucopus in the presence and absence of vegetative cover. Journal of Mammalogy 73:797-801.

Bent, A.C. 1932. Life histories of North American gallinaceous birds: orders Galliformes and Columbiformes. Smithsonian Institution U.S. National Museum, Bulletin 162. U.S. Government Printing Office, Washington, D.C.

Bjärvall, A., E. Nilsson, and L. Norling. 1977. The importance of old-growth forest for capercaillie and marten. Fauna Och Flora 72:31-38.

Boose, E. R., K. E. Chamberlin, and D. R. Foster. 2001. Landscape and regional impacts of hurricanes in New England. Ecological Monographs 7:27-48.

Boyle, J. R. 2000. Managing our grandchildren's forests: the role of soil biology and soil ecology. Pages 109-113 in Proceedings of the California Forest Soils Council Conference on Forest Soils Biology and Forest Management, February 23-24, 1996, Sacramento, California. PSW-GTR-178. USDA-Forest Service, Pacific Southwest Research Station, Albany, California.

Bromley, S. W. 1935. The original forest types of southern New England. Ecological Monographs 5:61-89.

Buchert, G. P., O. P. Rajora, J.V. Hood, and B. P. Dancik. 1997. Effects of harvesting on genetic diversity in old-growth eastern white pine in Ontario, Canada. Conservation Biology 11:747-758.

Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications 5:336-352.

Carey, A. B., T. M. Wilson, C. C. Maguire, and B. L. Biswell. 1997. Dens of northern flying squirrels in the Pacific Northwest. Journal of Wildlife Management 61:684-699.

Chandler, D. S. 1987. Species richness and abundance of Pselaphidae (Coleoptera) in old-growth and 40-year-old forests in New Hampshire. Canadian Journal of Zoology 65:608-615.

Chandler, D. S. 1991. Comparison of some slime-mold and fungus feeding beetles (Coleoptera: Eucinetoidea, Cucujoidea) in an old-growth and 40-year-old forest in New Hampshire. The Coleopterists Bulletin 45:239-256.

Chandler, D. S., and S. B. Peck. 1992. Diversity and seasonality of Leiodid beetles (Coleoptera: Leiodidae) in an old-growth and a 40-year-old forest in New Hampshire. Environmental Entomology 21:1283-1291.

Chapin, T. G., and D. J. Harrison. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. Conservation Biology 12:1327-1338.

Chapin, T. G., D. M. Phillips, D. J. Harrison, and E. C. York. 1997. Seasonal selection of habitats by resting marten in Maine. Pages 166-181 in G. Proulx, H. N. Bryant, and P. Woodard, editors. Martens: Taxonomy, ecology, techniques, and management. Provincial Museum of Alberta, Edmonton.

Cogbill, C.V. 1996. Black growth and fiddlebutts: The nature of old-growth red spruce. in M. B. Davis, editor. Eastern Old-Growth Forests: Prospects for rediscovery and recovery. Island Press, Washington, D.C.

Cogbill, C. 2000. Vegetation of the presettlement forests of northern New England and New York. Rhodora 102:250-276.

Cogbill, C.V., J. Burk, and G. Motzkin. 2002. The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys. Journal of Biogeography 29:1279-1304.

Constantine, D. G. 1966. Ecological observations on Lasiurine bats in Iowa. Journal of Mammalogy 47:34-41.

Corn, J. G., and M. G. Raphael. 1992. Habitat characteristics at marten subnivean access sites. Journal of Wildlife Management 56:442-448.

Cotton, C. L., and K. L. Parker. 2000. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. Journal of Mammalogy 81:1071-1086.

Dahir, S. E., and C. G. Lorimer. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. Canadian Journal of Forest Research 26:1875-1892.

Davis, M. B. 1996. Extent and location. Pages 18-32 in M. B. Davis, editor. Eastern old-growth forests: Prospects for rediscovery and recovery. Island Press, Washington, D.C.

Daw, S. K., and S. DeStefano. 2001. Forest characteristics of northern goshawk nest stands and post-fledging areas in Oregon. Journal of Wildlife Management 65:59-65.

DeGraaf, R. M., and M. Yamasaki. 2001. New England Wildlife: Habitat, Natural History, and Distribution. University Press of New England, Hanover, New Hampshire.

DeGraaf, R. M., M. Yamasaki, W. B. Leak, and J. W. Lanier. 1992. New England wildlife: management of forest habitats. USDA - Forest Service General Technical Report NE-144, Radnor, Pennsylvania.

deMaynadier, P. G., and M. L. Hunter, Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12:340-352.

Donovan, T. E., F. R. Thompson, III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380-1395.

Drew, G. S. 1995. Winter habitat selection by American marten (Martes americana) in Newfoundland: why old growth? Ph.D. Thesis. Utah State University, Logan, Utah.

Duffy, D. C., and A. J. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conservation Biology 6:196-201.

Dunwiddie, P. 1993. Survey of old-growth forests in Massachusetts, Final Report, February 3, 1993. Report to the Massachusetts Natural Heritage and Endangered Species Program, Westborough.

Dunwiddie, P., D. R. Foster, D. J. Leopold, and R. T. Leverett. 1996. Old-growth forests of southern New England, New York, and Pennsylvania. Pages 126-143 in M. B. Davis, editor. Eastern Old-Growth Forests: Prospects for rediscovery and recovery. Island Press, Washington, D.C.

Edmonds, R. L., J. L. Marra, A. K. Barg, and G. B. Sparks. 2000. Influence of forest harvesting on soil organisms and decomposition in western Washington. Pages 53- in Proceedings of the California Forest Soils Council Conference on Forest Soils Biology and Forest Management, February 23-24, 1996, Sacramento, California. PSW-GTR-178. USDA-Forest Service, Pacific Southwest Research Station, Albany, California.

Esseen, P.-A., K.-E. Renhorn, and R.B. Peterson. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecological Applications 6:228-238.

Fan, Z., S. R. Shifley, M. A. Spetich, F. R. Thompson, and D. R. Larsen. 2003. Distribution of cavity trees in midwestern old-growth and second-growth forests. Canadian Journal of Forest Research 33:1481-1494.

Fisk, M. C., D. R. Zak, and T. R. Crow. 2002. Nitrogen storage and cycling in old- and second-growth northern hardwood forests. Ecology 83:73-87.

Foster, D. R. 1988a. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah forest, south-western New Hampshire, U.S.A. Journal of Ecology 76:105-134.

Foster, D. R. 1988b. Species and stand response to catastrophic wind in central New England, U.S.A. Journal of Ecology 76:135-151.

Frelich, L. E., and C. G. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forests of the Upper Great Lakes region. Ecological Monographs 61:145-154.

Fuller, R. J. 2000. Influence of treefall gaps on distributions of breeding birds within interior old-growth stands in Bialowieza Forest, Poland. Condor 102:267-274.

Gerrow, J. S. 1996. Home range, habitat use, nesting ecology and diet of the northern flying squirrel in southern New Brunswick. M.S. thesis. Acadia University, Wolfville, Nova Scotia.

Gilbert, J. H., J. L. Wright, D. J. Lauten, and J. R. Probst. 1997. Den and rest-site characteristics of American marten and fisher in northern Wisconsin in G. Proulx, H. N. Bryant, and P. Woodard, editors. Martens: Taxonomy, Ecology, Techniques, and Management. Provincial Museum of Alberta, Edmonton, Alberta.

Gilliam, F. S., and M. R. Roberts. 2003. The herbaceous layer in forests of eastern North America. Oxford University Press, New York.

Goodburn, J. M., and C. G. Lorimer. 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. Canadian Journal of Forest Research 28:427-438.

Graber, R. E., and D. F. Thompson. 1978. Seeds in the organic layers and soil of four beech-birch-maple stands. Research Paper NE-401. USDA-Forest Service, Radnor, Pennsylvania.

Graveland, J., R. van der Wal, J. H. Van Balen, and A. J. Van Noordwijk. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. Nature 368:446-448.

Graveland, J., and T. Van Gijzen. 1994. Arthropods and seeds are not sufficient as calcium sources for shell formation and skeletal growth in passerines. Ardea 82:299-314.

Grove, S. J. 2002. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation 104:149-171.

Hagan, J. W., III, and D. W. Johnston, editors. 1992. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Haney, J. C. 1997. Spatial incidence of Barred Owl (Strix varia) reproduction in old-growth forest of the Appalachian Plateau. Journal of Raptor Research 31:241-252.

Haney, J. C. 1999. Hierarchical comparisons of breeding birds in old-growth conifer-hardwood forest on the Appalachian Plateau. Wilson Bulletin 111:89-99.

Haney, J. C., and C. P. Schaadt. 1996. Functional roles of eastern old growth in promoting forest bird diversity. Pages 76-88 in M. B. Davis, editor. Eastern Old-Growth Forests: Prospects for rediscovery and recovery. Island Press, Washington, D.C.

Hardt, R. A., and W. T. Swank. 1997. A comparison of structural and compositional characteristics of Southern Appalachian young second-growth, maturing second-growth, and old-growth stands. Natural Areas Journal 17:42-52.

Hargis, C. D., J. A. Bissonette, and D. L. Turner. 1999. The influence of forest fragmentation and landscape pattern on American martens. Journal of Applied Ecology 36:157-172.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S.V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Seddell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.

Harper, R. M. 1918. Changes in the forest area of New England in three centuries. Journal of Forestry 16:442-452.

Hicks, R. R., and J. Holt. 1999. Comparison of ecological characteristics of three remnant old-growth woodlots in Belmont County, Ohio. Pages 51-59 in 12th Central Hardwood Forest Conference: Proceedings of a meeting held at Lexington, Kentucky 28 February-March 2 1999. GTR SRS:24. USDA-Forest Service, Southern Research Station, Asheville, North Carolina.

Houle, G. 1992. The reproductive ecology of Abies balsamea, Acer saccharum and Betula alleghaniensis in the Tantaré Ecological Reserve, Québec. Journal of Ecology 80:611-623.

Humes, M. L., J. P. Hayes, and M. W. Collopy. 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. Journal of Wildlife Management 63:553-561.

Hura, C. R., and T. R. Crow. 2004. Woody debris as a component of ecological diversity in thinned and unthinned northern hardwood forests. Natural Areas Journal 24:57-64.

Jones, E. W. 1945. The structure and reproduction of the virgin forest of the north temperate zone. New Phytologist 44:130-148.

Jules, E. S. 1998. Habitat fragmentation and demographic change for a common plant: Trillium in old-growth forest. Ecology 79:1645-1656.

Jules, E. S., and B. J. Rathcke. 1999. Mechanisms of reduced Trillium recruitment along edges of old-growth forest fragments. Conservation Biology 13:784-793.

Jung, T. S., I. D. Thompson, R. D. Titman, and A. P. Applejohn. 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. Journal of Wildlife Management 63:1306-1319.

Komonen, A., R. Penttila, M. Lindgren, and I. Hanski. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90:119-126.

Leckie, S., M. Vellend, G. Bell, M. J. Waterway, and M. J. Lechowicz. 2000. The seed bank in an old-growth, temperate deciduous forest. Canadian Journal of Botany 78:181-192.

Leopold, D. J., C. Reschke, and D. S. Smith. 1988. Old-growth forests of Adirondack Park, New York. Natural Areas Journal 8:166-189.

Lesica, P., B. McCune, S.V. Cope, and W. S. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. Canadian Journal of Botany 69:1745-1755.

Likens, G. E., C. T. Driscoll, D. C. Buso, T. G. Siccama, C. E. Johnson, G. M. Lovett, T. J. Fahey, W. A. Reiners, D. F. Ryan, C. W. Martin, and S. W. Bailey. 1998. The biogeochemistry of calcium at Hubbard Brook. Biogeochemistry 41:89-173.

Lofroth, E. C. 1993. Scale dependent analyses of habitat selection by marten in the sub-boreal spruce biogeoclimatic zone, British Colombia. M.S. Thesis. Simon Fraser University, British Colombia, Canada.

Lorimer, C. G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. Ecology 58:139-148.

Lorimer, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169-1184.

Lorimer, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 Years of change. Wildlife Society Bulletin 29:425-439.

Lorimer, C. G., S. E. Dahir, and E.V. Nordheim. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. Journal of Ecology 89:960-971.

Maeto, K., S. Sato, and H. Miyata. 2002. Species diversity of longicorn beetles in humid warm-temperate forests: The impact of forest management practices on old-growth forest species in southwestern Japan. Biodiversity and Conservation 11:1919-1937.

Markewitz, D., D. D. Richter, H. L. Allen, and J. B. Urrego. 1998. Three decades of observed soil acidification in the Calhoun Experimental Forest: Has acid deposition made a difference? Soil Science Society of America Journal 62:1428-1439.

Marks, P. L., and S. Gardescu. 1992. Vegetation of the Central Finger Lakes Region of New York in the 1790s. Pages 1-35 in Late Eighteenth Century Vegetation of Central and Western New York State on the Basis of Original Land Survey Records. New York State Museum, Albany, NY.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94:199-209.

Marquis, D. A. 1975. Seed storage and germination under northern hardwood forests. Canadian Journal of Forest Research 5:478-484.

McGee, G. G., D. J. Leopold, and R. D. Nyland. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. Ecological Applications 9:1316-1329.

McLaughlin, S. B., and R. Wimmer. 1999. Calcium physiology and terrestrial ecosystem processes. New Phytologist 142:373-417.

Meier, A. J., S. P. Bratton, and D. C. Duffy. 1996. Possible ecological mechanisms for loss of vernal herb diversity in logged eastern deciduous forest. Ecological Applications 5:935-946.

Miller, T. F., D. J. Mladenoff, and M. K. Clayton. 2002. Old-growth northern hardwood forests: spatial autocorrelation and patterns of understory vegetation. Ecological Monographs 72:487-503.

Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Conservation Biology 9:395-403.

Mladenoff, D. J. 1985. Dynamics of soil seed banks, vegetation, and nitrogen availability in treefall gaps. Ph.D. Dissertation. University of Wisconsin, Madison.

Mladenoff, D. J., M. A. White, J. Pastor, and T. R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications 3:294-306.

Moldenke, A., M. Pajutee, and E. Ingham. 2000. The functional roles of forest soil arthropods: the soil is a lively place. Pages 7-22 in Proceedings of the California Forest Soils Council Conference on Forest Soils Biology and Forest Management, February 23-24, 1996, Sacramento, California. PSW-GTR-178. USDA-Forest Service, Pacific Southwest Research Station, Albany, California.

Mowrey, R.A. and J.C. Zasada. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. Pages 351-356 in W. R. Mechan, T. R. Merrell, Jr., and T. A. Hanley, editors. Fish and wildlife relationships in old-growth forests: proceedings of a symposium, Juneau, Alaska, April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Muller, R. N., and Y. Liu. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Canadian Journal of Forest Research 21:1567-1572.

Nakagoshi, N. 1984. Ecological studies on the buried viable seed population in soil of the forest communities of Miuajima Island, southwestern Japan. II. Hikobia 9:109-122.

Nakagoshi, N. 1985. Buried viable seeds in temperate forests. Pages 551-570 in J. White, editor. The Population Structure of Vegetation. Junk, Dordrecht.

Nakashizuka, T. 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology 70:1273-1278.

Neitlich, P. N. 1993. Lichen abundance and biodiversity along a chronosequence from young managed stands to ancient forest. Thesis. University of Vermont, Burlington, Vermont.

Nichols, G. E. 1913. The vegetative survey of Connecticut II. Virgin forests. Torreya 13:199-215.

Niemelä, J. 1997. Invertebrates and boreal forest management. Conservation Biology 11:601-610.

Ontario Ministry of Natural Resources. 2003. Old growth forest definitions for Ontario. Queen's Printer for Ontario, Toronto.

Oosting, H. F., and M. E. Humphreys. 1940. Buried viable seeds in successional series of old fields and forest soils. Bulletin of the Torrey Botanical Club 67:253-273.

Perault, D. R., and M.V. Lomolino. 2000. Corridors and mammal community structure across a fragmented, old-growth forest landscape. Ecological Monographs 70:401-422.

Peterson, C. J., and S. T. A. Pickett. 2000. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. Oikos 90:489-500.

Petranka, J. W., P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67:135-147.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on Southern Appalachian salamanders. Conservation Biology 7:363-370.

Pickett, S. T. A., and M. J. McDonnell. 1989. Seed bank dynamics in temperate deciduous forest. Pages 123-147 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. Ecology of Soil Seed Banks. Academic Press, San Diego.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.

Pyare, S., and W. S. Longland. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681-689.

Richter, D. D. 2000. Soil and water effects on modern forest harvest practices in North Carolina. Available at URL http://www.env.duke.edu/scsf/. Southern Center for Sustainable Forests. North Carolina State University College of Forest Resources, Duke University School of the Environment, and North Carolina Department of Environment and Natural Resources.

Rooney, T. P., and W. J. Dress. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania, USA. Natural Areas Journal 17:297-305.

Rose, F. 1992. Temperate forest management: its effects on bryophyte and lichen floras and habitats. Pages 211-233 in J. W. Bates, and A. M. Farmer, editors. Bryophytes and Lichens in a Changing Environment. Clarendon, Oxford.

Runkle, J. R. 1998. Changes in southern Appalachian canopy tree gaps sampled thrice. Ecology 79:1768-1780.

Runkle, J. R. 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. Ecology 81:554-567.

Schwarz, P. A., T. J. Fahey, C. W. Martin, T. G. Siccama, and A. Bailey. 2001. Structure and composition of three northern hardwood-conifer forests with differing disturbance histories. Forest Ecology and Management 144:201-212.

Seischab, F. K. 1990. Presettlement forests of the Phelps and Gorham Purchase in western New York. Bulletin of the Torrey Botanical Club 117:27-38.

Seischab, F. K. 1992. Forests of the Holland Land Company in western New York, circa 1798. Pages 36-53 in Late Eighteenth Century Vegetation of Central and Western New York State on the Basis of Original Land Survey Records. New York State Museum, Albany, NY.

Seischab, F. K., and D. Orwig. 1991. Catastrophic disturbances in the presettlement forests of western New York. Bulletin of the Torrey Botanical Club 118:117-122.

Sherburne, S. S., and J. A. Bissonette. 1994. Marten subnivean access point use: response to subnivean prey levels. Journal of Wildlife Management 58:400-405.

Siccama, T. G. 1971. Presettlement and present forest vegetation in northern Vermont with special reference to Chittenden County. American Midland Naturalist 85:153-172.

Smith, J. E., R. Molina, M. M. P. Huso, D. L. Luoma, D. McKay, M. A. Castellano, T. Lebel, and Y. Valachovic. 2002. Species richness, abundance, and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation-age, and old-growth stands of Douglas-fir (Pseudotsuga menziesii) in the Cascade Range of Oregon, U.S.A. Canadian Journal of Botany 80:186-204.

Speiser, R., and T. Bosakowski. 1987. Nest site selection by northern goshawks in northern New Jersey and southeastern New York. Condor 89:387-394.

Spence, J. R., D. W. Langor, J. Niemelä, H. A. Cárcamo, and C. R. Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. Annales Zoologici Fennici 33:173-184.

Spence, J. R., D. W. Langor, H. E. J. Hammond, and G. R. Pohl. 1997. Beetle abundance and diversity in a boreal mixedwood forest. Pages 285-299 in A. D. Watt and N. E. Stork, editors. Forests and insects: proceedings of the 18th Royal Entomological Society Symposium, 13-15 September 1995. Chapman and Hall, London.

Spencer, W. D., R. H. Barrett, and W. J. Zeielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management 47:1181-1186.

Spetich, M. A., S. R. Shifley, and G. R. Parker. 1999. Regional distribution and dynamics of coarse woody debris in Midwestern old-growth forests. Forest Science 45:302-313.

Stevenson, S. K. 1988. Dispersal and colonization of arboreal forage lichens in young forests. British Colombia Ministry of Forests, Integrated Wildlife Intensive Forestry Research (IWIFR) 38, Victoria, British Colombia, Canada.

Steventon, J. D., and J. T. Major. 1982. Marten use of habitat in a commercially clear-cut forest. Journal of Wildlife Management 46:175-182.

Thompson, I. D., H. A. Hogan, and W. A. Montevecchi. 1999. Avian communities of mature balsam fir forests in Newfoundland: Age-dependence and implications for timber harvesting. Condor 101:311-323.

Tyrrell, L. E., and T. R. Crow. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75:370-386.

Vellak, K., and J. Paal. 1999. Diversity of bryophyte vegetation in some forest types in Estonia: A comparison of old unmanaged and managed forests. Biodiversity and Conservation 8:1595-1620.

Vogelmann, H. W., J. D. Badger, M. Bliss, and R. M. Klein. 1985. Forest decline on Camel's Hump, Vermont. Bulletin of the Torrey Botanical Club 112:274-287.

Waters, J. R., K. S. McKelvey, C. J. Zabel, and D. L. Luoma. 2000. Northern flying squirrel mycophagy and truffle production in fir forests in northeastern California. Pages 73-97 in Proceedings of the California Forest Soils Council Conference on Forest Soils Biology and Forest Management, February 23-24, 1996, Sacramento, California. PSW-GTR-178. USDA-Forest Service, Pacific Southwest Research Station, Albany, California.

Welsh, C. J. E., and D. E. Capen. 1992. Availability of nesting sites as a limit to woodpecker populations. Forest Ecology and Management 48:31-41.

Welsh, H. H., Jr. 1990. Relictual amphibians and old-growth forests. Conservation Biology 4:309-319.

Whitney, G. G. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old growth hemlock-white pine-northern hardwood stand. Ecology 65:403-408.

Whitney, G. G. 1994. From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America 1500 to Present. Cambridge University Press, New York.

Woods, K. D. 2000a. Dynamics in late-successional hemlock-hardwood forests over three decades. Ecology 81:110-126.

Woods, K. D. 2000b. Long-term change and spatial pattern in a late-successional hemlock-northern hardwood forest. Journal of Ecology 88:267-282.

Wynne, K. M., and J. A. Sherburne. 1984. Summer home range use by adult marten in northwestern Maine. Canadian Journal of Zoology 62:941-943.

Gustav W. Verderber

Spotted salamander and wood frog eggs

Blake Gardner

Gifford Woods Natural Area: *This 400 year-old maple has deep character lines weathered into its once-smooth bark, and growing fungi hint that its end is near.*

VERMONT
NATURAL
RESOURCES
COUNCIL
VERMONT'S ENVIRONMENTAL
GUARDIAN SINCE 1963

9 Bailey Avenue
Montpelier, VT 05602