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Forest Ecology and Management 185 (2003) 41–64

Forest Ecology and Management

www.elsevier.com/locate/foreco

Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions

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Abstract

Recent declines in the amount of habitat suitable for early successional wildlife in the northeastern US have prompted public land managers to consider establishing minimum levels of young forest, based on the natural range of variation, in order to maintain viable populations of these species. In this paper, we review evidence on the frequency, severity, and scale of natural disturbances in four major forest regions of the northeastern US. Using six independent lines of evidence, we examined the influence of natural disturbances in presettlement and modern times. In situations where estimates of annual disturbance rates were available, we estimated the regional age distribution of forest stands based on the assumption of random spatial pattern of disturbance. Available evidence suggests a gradient of generally decreasing disturbance frequency from coastal regions to the interior uplands and mountains. The proportion of the presettlement landscape in seedling–sapling forest habitat (1–15 years old) ranged from 1 to 3% in northern hardwood forests (*Fagus–Betula–Acer–Tsuga*) of the interior uplands to possibly >10% in coastal pine–oak (*Pinus–Quercus*) barrens. Within a region, variability in the amount of young forest is not well known, but upper slopes and ridges generally had the highest disturbance frequency and severity. Comparison of line transect data of the presettlement land surveys with modern plot surveys suggests that present-day amounts of young forests in northern hardwood and spruce–hardwood forests in some regions may be several times higher than in presettlement times. In coastal oak forests and pine–oak barrens, the amount of young forests and open woodlands may be less because of reduced fire frequency.

Keywords: Blowdowns; Early successional habitat; Fire regimes; Insect epidemics; Natural disturbances; Old-growth forests; Presettlement forests; Windthrow

1. Introduction

Historical land-use changes in the eastern US, as in many other parts of the world, have caused extreme swings in forest habitat conditions. In the late 19th and early 20th centuries, much of the northeast was dominated by young forest stands as a legacy of extensive logging, land clearing, fuelwood utilization, repeated fires on cutover land, and widespread farm abandonment. For example, >75% of the forest in central Massachusetts was less than 30 years old in 1885 (Foster et al., 1998). Government surveys in 1908 revealed that 56% of the forest land in 12 eastern states was classified as "cutover land" (Whitney,

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0378-1127/$ – see front matter
doi:10.1016/S0378-1127(03)00245-7

1994, p. 192). Subsequent declines in the rate of forest utilization allowed many forests in eastern US to recover (McKibben, 1995). As these regenerating forests have matured, a number of animal populations also recovered that were uncommon a hundred years ago (Kendeigh, 1946; Whitney, 1994).

Concurrent with the maturation of second-growth stands, the abundance of early successional habitats has declined in much of the northeast. Seedling–sapling stands currently represent 4–18% of forests in the region (Trani et al., 2001). Yet the effects of the reduction in habitat on wildlife species that require young forests have received relatively little attention. As Askins (2001) has pointed out, shrublands, clearcuts, and thickets are ''unpopular habitats'' among the general public. There is also a widespread notion, even among some conservation groups, that wildlife species dependent on early successional habitats are ''weedy generalists'' that thrive in human-dominated habitats and therefore require no special conservation measures. However, substantial population declines have occurred among early successional obligates. For example, of the 126 neotropical migrant bird species in the northeast, 74 require disturbance-generated habitats or young forests, and these species are scarce or absent in mature and old-growth stands (Smith et al., 1993). Thompson and DeGraaf (2001) pointed out that no breeding bird species are dependent upon uneven-aged stands, whereas many species require even-aged habitats. Among the disturbance-dependent bird species throughout eastern North America, Hunter et al. (2001) predicted that if early successional habitats continue to decline, many species will be extirpated from portions of the eastern US and others risk extinction. Fourteen of these species are federally listed as endangered or threatened, and 18 others are on a national watch list (Hunter et al., 2001).

Broader-level landscape considerations also are important in maintaining suitable conditions. Because early successional species utilize habitats that persist only for a short time, continual turnover of stands somewhere on the landscape is necessary. In addition to the total amount of young-forest habitat, the scale of disturbance also is an important consideration. For example, prairie warblers (*Dendroica discolor*) and yellow-breasted chats (*Icteria virens*) will utilize moderate or large patches of habitat, but apparently avoid small openings (Annand and Thompson, 1997).

The wide historical swings in habitat conditions have prompted ecologists to consider appropriate historical benchmark conditions in the amount of early and late-successional habitats. Although natural disturbance regimes in the post-glacial era have fluctuated (e.g., Anderson et al., 1986), managing landscapes within a natural range of variability may help sustain population viability by maintaining landscape characteristics to which the regional plants and animals have become adapted (Seymour and Hunter, 1999; Thompson and DeGraaf, 2001). An understanding of natural disturbance regimes is also needed to fulfill the broader goals of ecosystem management on public lands (Thomas, 1996). Therefore, the purpose of our paper is to review evidence on the frequency, severity, and scale of natural disturbances in the major forest regions of the northeastern US. In regions with sufficient evidence, we provide estimates of the relative amount of young and old forest in presettlement times, but the temporal scope of the paper includes evidence spanning a broader period of several thousand years to characterize the range of variability.

A distinction is made in this paper between natural disturbances (caused by lightning, windstorms, insect outbreaks, etc.) and anthropogenic disturbances caused by Native Americans and European settlers, although these causes are often not distinguishable using historical or scientific evidence. Some disturbances in modern times also are discussed in situations where these events clarify the potential scope and impacts of natural disturbance, even though they may be operating on landscapes considerably affected by humans. However, analysis of recent anthropogenic disturbances such as logging, land clearing, and invasion of exotic species lies beyond the scope of this paper. Some types of anthropogenic disturbance (e.g., logging, grazing, prescribed burning) may be useful in conserving species at risk and are covered in other papers in this issue (cf. Foster and Motzkin, 2003; DeGraaf and Yamasaki, 2003; Litvaitis, 2003).

2. Investigative methods and limitations

2.1. Methods of analyzing disturbance frequency

There are six principal methods or sources that can be used to investigate natural disturbance regimes.

These include analysis of sedimentary pollen and charcoal (e.g., Patterson and Backman, 1988; Clark and Royall, 1995a), presettlement land survey records (Siccama, 1971; Cogbill, 2000), early descriptions by travelers, naturalists, and foresters (Day, 1953; Whitney, 1994), reconstructions of disturbance history in old-growth stands (Lorimer and Frelich, 1989; Chokkalingam, 1998), modern records and aerial photos (Fahey and Reiners, 1981; Jenkins, 1995), and computer modeling (Frelich and Lorimer, 1991a; Boose et al., 2001). Each method contributes unique information, but also has limitations. For example, paleoecological evidence from lakes and small forest hollows provides the only long-term record of fire activity, often extending over thousands of years, but it is often difficult to distinguish individual fires and usually not feasible to determine size or spatial extent. On the other hand, it is possible to map the boundaries of large fires in reasonable detail using presettlement land survey records, but the sampling period for this method spans only a few decades. There also are site and geographic limitations for most methods, as well as interpretive ambiguities and possible methodological biases. For example, remnant old-growth stands are rare and often restricted to steep or inaccessible topography that may not be representative of the larger landscape. Fortunately, the strengths of one method can often be used to compensate for the limitations of another, so that a synthesis of multiple lines of evidence often provides an excellent overview of disturbance regimes in a region. Nevertheless, there are still some large gaps in the record. In the best cases, there may be sufficient systematic evidence to estimate the proportion of the landscape in young forest habitat, but usually only for a short period prior to settlement or for a specific type of disturbance.

2.2. Estimating forest age structure on the presettlement landscape

For each forest type, we harmonized the evidence obtained from various methods to provide an integrated summary on disturbance regimes. In situations where quantitative information was available, we have provided preliminary pooled estimates of mean annual disturbance rates for the major categories of disturbance (primarily wind and fire) within a forest type. The composite figure was then used to estimate the proportion of the presettlement landscape in each of several forest age classes. These estimates should be considered region-wide averages, as the evidence in most cases is not sufficient to quantify local variation.

Estimates of regional forest age distribution based on annual disturbance rates are influenced by assumptions about the spatial pattern of disturbances. If stands are heavily disturbed only after they reach the rotation age (as, for example, in even-aged forest management), the resulting landscape age distribution is uniform, with an equal proportion of the landscape in each age class. However, if the pattern of disturbance is random (all stands have the same probability of disturbance in a given year regardless of age), even young stands can be disturbed again, and some old stands can escape disturbance for long periods by chance. This leads to a landscape with fewer young stands and more old stands than under the uniform assumption. The rotation period in these situations does not correspond to the maximum stand age, but rather the mean age. With the random distribution of disturbances, the age distribution of a forest landscape approaches a negative exponential curve, and 37% of the stands are actually older than the rotation period (Van Wagner, 1978).

Empirical age distributions from the boreal forest and conifer forests of western North America—landscapes dominated by stand-replacing fires—generally do follow a descending curve (Yarie, 1981; Johnson et al., 1995; Reed et al., 1998). This evidence suggests at least a quasi-random pattern of burned areas, and overlapping burns and reburns have been reported (Brown and Davis, 1973). Landscape age models have not been extensively investigated in temperate hardwood or mixed conifer–hardwood forests of the eastern US. But it is clear from the fire history of Maine, for example, that overlapping burns and reburns have been very common (Coolidge, 1963). Therefore, it seems reasonable to apply the negative exponential model as a first approximation to spruce–hardwood forests of northern New England.

Young forest stands are much less susceptible to windthrow than mature and old stands (Foster, 1988b). But there is little reason to think that wind will only blow down stands near the end of the rotation period, especially when the rotation period is 1000 years or more. In our initial empirical trials, an assumption of zero probability of windthrow for stands younger than 45 years had negligible effects on the estimated amount of young forest. In the final analyses (Tables 1–3), we used a simple negative exponential model in which the annual disturbance rate p is the pooled disturbance rate for both catastrophic windthrows and stand-replacing fires. Pooling these rates in the negative exponential model allows random (and overlapping) spatial patterns

Table 1
Expected percentage of regional landscape occupied by different age classes of northern hardwood forest under various rotation periods and assumptions about disturbance spatial patterns[a]

Age class	500-year rotation (fire 1000 years, wind 1000 years)		1364-year rotation (fire 3000 years, wind 2500 years)	
	Uniform	Random	Uniform	Random
Seedling–sapling (1–15 years)	3.0	3.0	1.1	1.1
Small pole (15–30 years)	3.0	2.9	1.1	1.1
Large pole (30–60 years)	6.0	5.5	2.2	2.1
Mature even-aged (60–100 years)	8.0	6.8	2.9	2.8
Old even-aged (100–150 years)	10.0	7.8	3.7	3.4
Transitional uneven (150–300 years)	30.0	19.2	11.0	9.3
Old uneven-aged (300+ years)	40.0	54.9	78.0	80.2

[a] Uniform refers to spatially non-overlapping disturbances that occur only when the stand has reached the rotation age. Random signifies a random spatial pattern in which all age classes have an equal probability of disturbance (see text).

Table 2
Expected percentage of regional landscape occupied by different age classes of spruce–northern hardwood forest under various rotation periods and assumptions about disturbance spatial patterns (see text)

Age class	230-year rotation (fire 385 years, wind 575 years)		335-year rotation (fire 800 years, wind 575 years)		388-year rotation (fire 1200 years, wind 575 years)	
	Uniform	Random	Uniform	Random	Uniform	Random
Seedling–sapling (1–15 years)	6.5	6.3	4.5	4.4	3.9	3.8
Small pole (15–30 years)	6.5	5.9	4.5	4.2	3.9	3.6
Large pole (30–60 years)	13.0	10.7	9.0	7.8	7.8	6.9
Mature even-aged (60–100 years)	17.4	12.3	12.0	9.4	10.3	8.4
Old even-aged (100–150 years)	21.8	12.6	14.9	10.3	12.9	9.3
Transitional uneven (150–200 years)	21.8	10.2	14.9	8.9	12.9	8.2
Old uneven-aged (200+ years)	13.0	42.0	40.2	55.0	48.3	59.8

Table 3
Expected percentage of regional landscape occupied by different age classes of spruce–northern hardwood forest under various rotation periods and assumptions about disturbance spatial patterns (continued)[a]

Age class	545-year rotation (fire 1200 years, wind 1000 years)		606-year rotation, mixed uplands (fire 800 years, wind 2500 years)		210-year rotation, swamps and flats (fire 800 years, wind 285 years)	
	Uniform	Random	Uniform	Random	Uniform	Random
Seedling–sapling (1–15 years)	2.8	2.7	2.5	2.4	7.1	6.9
Small pole (15–30 years)	2.8	2.6	2.5	2.4	7.1	6.4
Large pole (30–60 years)	5.6	5.1	5.0	4.6	14.2	11.6
Mature even-aged (60–100 years)	7.3	6.3	6.6	5.8	19.0	13.0
Old even-aged (100–150 years)	9.2	7.3	8.2	6.7	23.8	13.2
Transitional uneven (150–200 years)	9.2	6.7	8.2	6.2	23.8	10.4
Old uneven-aged (200+ years)	63.1	69.3	67.0	71.9	4.8	38.5

[a] The last two columns provide preliminary estimates for two broad habitat types: mixed spruce–hardwood forest on uplands and conifer-dominated sites in swamps and stony flats.

for both types of disturbance; stands blown down by wind can be burned at any subsequent time during the rotation period, and areas burned can later be windthrown. Following the approach of Van Wagner (1978), the cumulative proportion of the landscape in age classes up to age x, given an annual disturbance rate p, is calculated as

$$\sum f(x) = 1 - e^{-px}$$

In our analyses, the transition period from even-aged to uneven-aged stands is assumed to begin about 150 years after catastrophic disturbance, based on average life expectancy data for major tree species in the region (Moesswilde, 1995; Chokkalingam, 1998; Tyrrell et al., 1998).

3. Pine–oak barrens

Pine–oak barrens in the northeast are commonly dominated by pitch pine (*Pinus rigida*) with varying amounts of canopy oaks (e.g., *Quercus alba*), scrub oaks (e.g., *Q. ilicifolia*), and ericaceous shrubs (e.g., *Gaylussacia* and *Vaccinium* spp.). They are commonly associated with the sandy soils of the Coastal Plain (Lull, 1968) or similar soils inland; they may also be found on rocky ridges and hilltops. Although pine barrens typically occupy droughty, nutrient-poor sites, average annual precipitation (102–122 cm) is similar to that of other community types in the region (Lull, 1968). Temperatures are moderate with a typical frost-free growing season of 180–210 days (Lull, 1968).

Proximity of pine–oak barrens to the coast facilitated early exploitation by European settlers, so detailed presettlement records of species composition and disturbance patterns are lacking. However, there are some general descriptions, such as that of a surveyor in 1687, who described the pine barrens of southeastern New Jersey as ‘‘a great tract of barren lands consisting of pine land and sand’’ (Wacker, 1979). Paleoecological data confirm that pines and oaks dominated for many centuries prior to European settlement (Florer, 1972; Watts, 1979; Fuller et al., 1998; Parshall et al., 2003), although in some areas pitch pine replaced white pine (*Pinus strobus*) and oaks as a result of logging, burning, and plowing by European settlers (Patterson and Backman, 1988).

Of the tree-dominated communities in the northeast, the pine–oak barrens are often considered the most fire prone. Sediment cores often contain abundant presettlement charcoal, sometimes in quantities comparable to post-settlement times (Patterson and Backman, 1988; Fuller et al., 1998; Copenheaver et al., 2000; Parshall et al., 2003). Recorded fires in recent centuries have been frequent and often large. In the New Jersey pine barrens, Forman and Boerner (1981) reported that a few fires had burned >40,000 ha each during the last 150 years, with large fires more commonly ranging from 8000–16,000 ha. Individual fire years in which >50,000 ha burned (~10% of the total area) occurred about once every 20 years. Local variation in fire regimes was noted due to the distribution of natural fire breaks (e.g., swamps), community composition, and weather patterns. Pine–oak barrens in other portions of the northeast may have experienced smaller fires, partly because of their smaller total contiguous area. Even so, individual fires of more than 1000 ha have been reported (Schweitzer and Rawinski, 1988). Humans, both Native Americans and European settlers, were the primary ignition sources, as lightning fires are uncommon in the northeastern barrens (Lutz, 1934; Forman and Boerner, 1981).

Quantitative estimates of natural fire frequencies for northeastern pine–oak barrens are not available, and the only estimates are based on relatively recent historical records. Using different approaches, both Lutz (1934) and Forman and Boerner (1981) estimated an average return interval (for mostly intense fires that open the canopy) of approximately 20 years for the late 1800s and early 1900s. The average return interval had increased to about 65 years by the mid-1970s (Forman and Boerner, 1981). The return interval was estimated to only be 8 years for the ‘‘Plains’’, an area within the New Jersey pine barrens characterized by short (<4 m), sprout-origin pines and oaks (Lutz, 1934). Although pine–oak barrens often succeed to a mature forest of oaks in the absence of fire (Little, 1979), harsh site conditions can sometimes keep barrens in an early successional state for prolonged periods. Winne (1997) reported that an area of barrens in eastern Maine has remained open since created by a major fire 1700 years ago.

Of the four major forest types and geographic regions in the northeast, the pine–oak barrens probably had the highest incidence of severe disturbance, mostly from fires and secondarily from periodic hurricanes. As a result, pine–oak barrens may have had the highest proportion of land area in recently disturbed habitat and young forest suitable for early successional wildlife. The lack of quantitative evidence on stand-replacing fires prior to European settlement precludes an estimate of the expected proportion of the landscape in young forest habitat under natural conditions. Therefore, we simply note that return intervals spanning a broad range of 40–150 years for severe fires would yield estimates of 10–31% of the landscape in the seedling–sapling stage (stand ages of 1–15 years) under the assumption of a random spatial pattern of ignitions.

4. Eastern oak forests

Forests dominated by oaks and hickories (*Carya* spp.) are dispersed across eight distinct physiographic and soil regions in the northeast, from unconsolidated sandy soils of the coastal plain to the predominantly stony loam and sandy loam soils on steep slopes of the Allegheny Mountains. However, the boundaries of the region correspond well with climatic variables, especially a mean frost-free period of 150–180 days (Lull, 1968).

Oaks of all species made up 35–75% of the witness trees in presettlement land surveys, usually accompanied by hickories, chestnut (*Castanea dentata*), and pines (e.g., Russell, 1981; Abrams and Ruffner, 1995; Black and Abrams, 2001). Paleoecological studies indicate oak dominance has been remarkably stable over the past 9000 years in most areas (Watts, 1979; Maenza-Gmelch, 1997). In recent decades, however, oak forests have developed dense understories of shade-tolerant species, including maples (*Acer* spp.) and beech (*Fagus grandifolia*) (Lorimer, 1984; Abrams, 1992). These shade-tolerant species may be capable of displacing oaks on some mesic and dry-mesic sites (Abrams and Downs, 1990; Abrams and Nowacki, 1992).

4.1. Windstorms

Atlantic hurricanes are one of the principal disturbance agents in parts of the oak region. Although hurricanes begin to lose energy as they move inland or move across cold ocean currents (e.g., Gulf of Maine), some hurricanes move northward across Long Island and into interior New England, causing severe damage even 100 km from the coast. Damage can range from light crown damage and scattered treefalls to nearly complete blowdown of forest stands. Boose et al. (2001) documented 67 New England hurricanes that occurred from 1620 to 1997, averaging one storm every 6 years. At the Harvard Forest in central Massachusetts, three hurricanes reached or exceeded F2 intensity, sufficient to cause blowdown of entire stands, with a mean recurrence of 150 years. Using historical reports on damage to calibrate a hurricane simulation model, Boose et al. (2001) provided evidence of a geographical gradient in mean recurrence of hurricane damage, ranging from 85 years for F2 damage in southern coastal New England to more than 380 years for F2 damage in northern Maine (Fig. 1).

Studies at a local scale have revealed a number of factors that may explain variation in the degree of disturbance caused by hurricanes. In central Massachusetts, stands on level ground or on windward slopes (S, SE, E) were exposed to the brunt of the storm and had the highest levels of damage after the hurricane of

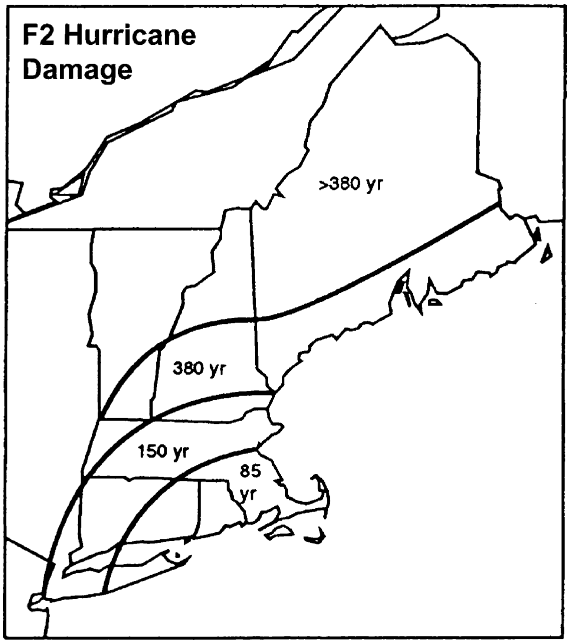

Fig. 1. Zones of hurricane frequency in New England, showing mean recurrence intervals between consecutive F2 hurricanes capable of causing extensive blowdown of forest stands (from Boose et al., 2001; reproduced with permission of the Ecological Society of America).

1938 (F2+ intensity). The storm had less effect on leeward slopes (W, NW, N). Damage varied by species composition and tree size. Uprooting and trunk breakage were greater in conifer stands than in hardwoods, but were generally high in mature stands >15 m tall. Mature conifer stands averaged >75% mortality of canopy trees on exposed sites, and often had >50% tree mortality on protected sites. Mature hardwood stands, in contrast, had 50–75% tree mortality on exposed sites, but <25% tree mortality on protected sites (Fig. 2). Young stands (only 10 m tall) had 25–75% damage depending on species composition and slope exposure (Foster and Boose, 1992).

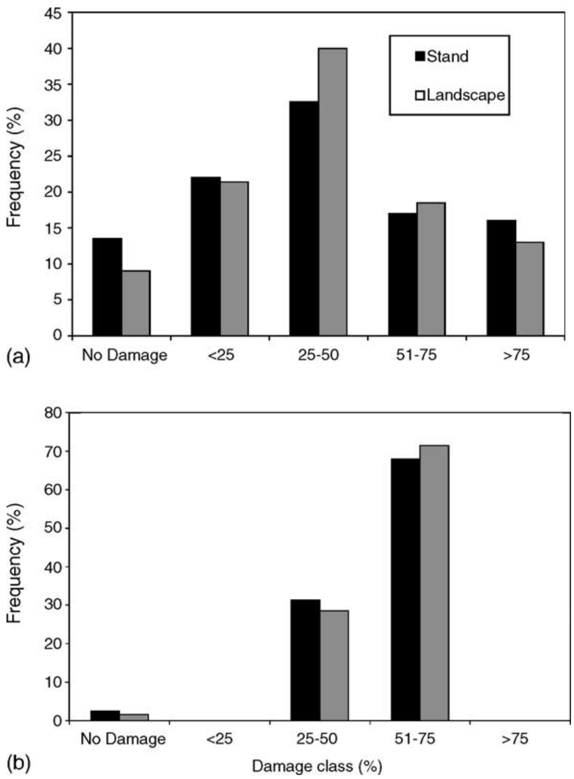

Fig. 2. Proportions of the landscape in central Massachusetts in different forest damage classes after the 1938 hurricane. The graphs show the predicted outcome of various scenarios based on a landscape model calibrated with actual stand damage data. (a) Percentage of stands (dark bars) and percentage of landscape area (stippled bars) in various damage classes for hardwood stands based on observed 1938 stand heights. (b) Distribution of hardwood stand damage classes expected if all stands were mature with a uniform height of 20 m (from Foster and Boose, 1992; reproduced with permission from the British Ecological Society).

Topographic variation, therefore, leads to landscape heterogeneity in forest age class distribution because of variations in slope exposure, physiographically influenced differences in forest species composition, and pre-existing variation in stand ages. In the gently rolling portions of southern and central New England, most of the landscape would be rated as exposed or vulnerable to the effects of intense hurricanes. For example, 82% of the landscape of the town of Petersham in central Massachusetts was classified as exposed to the storm tracks of the three F2 hurricanes that had occurred there since 1620 (Boose et al., 2001). If old-field pine stands are included, the 1938 hurricane caused >75% canopy-tree mortality on nearly 40% of the landscape and >50% mortality on 60% of the landscape. About 25% of the landscape had light damage (<25% mortality), and only 15% had no damage (Foster and Boose, 1992).

Despite the battered condition of the landscape after exposure to an F2 hurricane, there is considerable small-scale variability in the condition of stands. Few storms are powerful enough to blow down all the trees over a large area (Boose et al., 2001). The resulting mosaic of stands with light, moderate, and heavy damage creates conditions suitable for a wide variety of organisms that depend on a range of seral stages. Most of the lightly damaged stands can restore full crown cover within a decade or two, and hence become refugia for late-successional species in the battered, post-hurricane landscape. However, the long intervals (e.g., 150 years) between these powerful, stand-replacing hurricanes probably results in erratic population cycles for some early successional species. In the intervening decades, the more mobile species must seek out patches of disturbed habitat caused by thunderstorm winds, floods, ice storms, and forest fires.

For oak stands distant from the coast (e.g., central Pennsylvania), other types of windstorms such as thunderstorm downbursts are probably an important feature of the natural disturbance regime. Tornadoes are rare, with an estimated mean point recurrence interval of 10,000–20,000 years (Whitney, 1994).

4.2. Fire regimes

Most fires in oak forests occur in early spring and late fall after the leaves have been shed. At these times herbaceous vegetation is largely in a cured stage and the bare tree crowns allow direct sunlight to dry out the ground fuels on dry, windy days. Fire intensity is enhanced by the loose, porous leaf litter of curled oak leaves, the retention of some dead oak leaves on trees overwinter, and the presence in some areas of flammable shrubs such as *Kalmia latifolia*. Gusty winds can blow the burning leaves ahead of the main fire front, igniting spot fires that help accelerate fire spread and area burned.

The earliest explorers and colonists of the oak–hickory region described rather open, park-like woods free of dense undergrowth and sometimes with abundant grass (see reviews by Day, 1953; Russell, 1983; Whitney, 1994; Lorimer, 1993, 2001). The surveyor Peter Lindestrom wrote in 1656 that in eastern Delaware, ''there indeed grows a great deal of high grass, which reaches above the knees of a man . . . there is also no thickly grown forest but the trees stand far apart, as if they were planted'' (Lindestrom, 1656). In 1684, Lawrie noted that in eastern New Jersey ''the trees grow generally not thick, but in some places ten, in some fifteen, and in some twentyfive or thirty upon an acre'' (Whitney, 1994, p. 118). Very similar descriptions of park-like oak woodlands were made in coastal Massachusetts (Morton, 1632; Wood, 1634; Whitney, 1994), portions of the southern Maine coast (Rosier, 1605; Grant, 1946; Day, 1953), the Connecticut Valley of Massachusetts, and the Lake Ontario lowlands of western New York (Maude, 1826; Day, 1953).

The openness of the woodlands was often attributed by early observers to intentional burning by native tribes (e.g., Morton, 1632; Van der Donck, 1656). Because mature oak forests normally develop closed canopies and very dense understories of woody shrubs and saplings (e.g., Nowacki and Abrams, 1992), and lightning fires are infrequent (Patterson and Sassaman, 1988; Schroeder and Buck, 1970), anthropogenic burning is probably necessary to maintain open woodlands on moderately productive sites. Early descriptions suggest that uncontrolled fires in the 17th century were often moderately intense (e.g., Morton, 1632; Van der Donck, 1656). Regardless of their cause, these wildfires were more likely to create open habitats suitable for early-successional animals than would a series of modern, low-intensity prescribed burns.

Because of their anecdotal nature, these early descriptions do not permit quantitative estimates of the proportion of the landscape dominated by open woodlands. Geographical and temporal biases are also likely to influence these observations. Most early descriptions were obtained from the first-settled regions along the seacoast and in the major river valleys. Because Native American villages were heavily concentrated in these same areas (Fig. 3), open woodlands and savanna-like vegetation could have been localized and largely restricted to areas of relatively high human population density (Russell, 1983; Patterson and Sassaman, 1988; Whitney, 1994). Villages, however, were less than 20–40 km apart in most areas (Fig. 3). Annual use of fire to drive game on hunting grounds between the villages could easily have had a major impact on the general landscape, depending on average fire size.

There are unfortunately few if any good early descriptions of the interior upland vegetation. By the time the interior zones were settled, the novelty in describing North American vegetation for a European audience had worn off, and few people continued to write detailed descriptions. Furthermore, the initiation of widespread trade and warfare between Native Americans and Europeans altered the aboriginal way of life, including village size and location, patterns of hunting, and possibly fire use (Russell, 1983; Foster and Motzkin, 2003). Conceivably, the late 17th and 18th century reports of open woodlands may have reflected a relatively late development in response to increased trade and warfare. Other lines of evidence are therefore needed to resolve these ambiguities.

Presettlement land survey records in the oak region are early ''metes and bounds'' surveys and contain little or no direct evidence on disturbance or forest developmental stage. However, the witness trees used to mark survey boundaries do preserve some important indirect evidence of fire frequency over a vast portion of the otherwise little-known interior uplands. Surveys in the eastern half of Pennsylvania and northern New Jersey show that shade-tolerant, late-successional species were a remarkably minor component of the presettlement forest, generally making up <7% of the witness trees except in the high plateaus and mountains (Russell, 1981; Abrams and Downs, 1990; Abrams and Nowacki, 1992; Abrams and Ruffner, 1995; Black and Abrams, 2001). Yet the modern forests on similar sites face strong successional pressures toward canopy dominance by shade-tolerant species (Abrams and Downs,

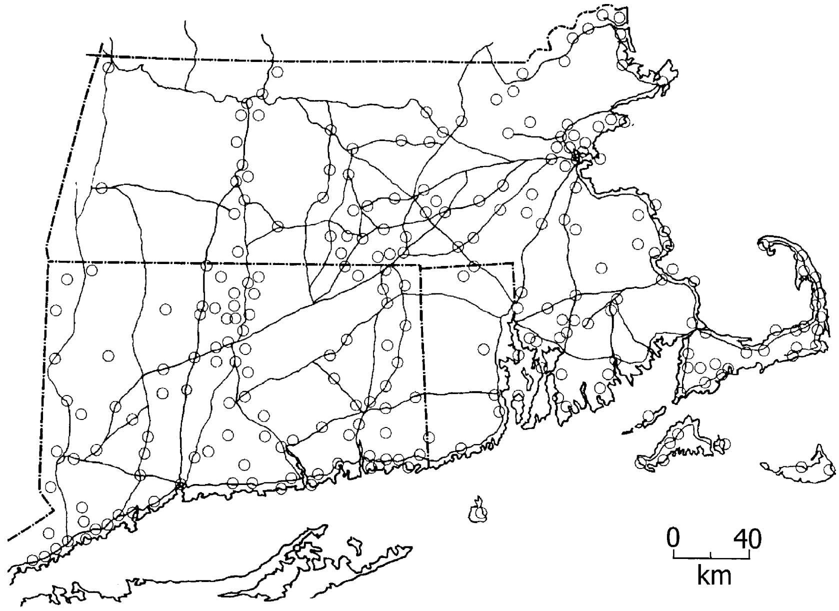

Fig. 3. Map of recorded Native American village sites (circles) and trails in southern New England at the beginning of the 17th century. The highest concentration of village sites, and probably the greatest amount of fire-influenced oak woodland, occurred in coastal areas and major river valleys (from Russell, 1980; reproduced with permission of the University Press of New England).

1990; Abrams and Nowacki, 1992). The low abundance of tolerant species in presettlement times is readily explainable if fires in the interior uplands were widespread and at least moderately frequent (cf. Grimm, 1984; Leitner et al., 1991 for clear analogs in the midwestern US), but is less easily explained if presettlement fires are presumed to have been infrequent or patchy in their occurrence. Climate change may also have been a factor, but oak forests of much drier climates such as southwest Wisconsin and central Missouri have also not been self-perpetuating on mesic sites and likewise have been succeeding toward shade-tolerant species (Pallardy et al., 1988; Hix and Lorimer, 1991).

A more direct approach to investigating presettlement fire frequency is the analysis of fire scars in old-growth stands or on remnant old (legacy) trees scattered in a matrix of second-growth forest. Detailed and systematic work of this type has been done only recently by Shumway et al. (2001) for an old-growth oak forest on steep slopes above the Savage River in western Maryland and by Dey and Guyette (2000) in nine oak–pine stands in southern Ontario. Both studies revealed a high presettlement frequency of fires, with mean surface-fire intervals of 6–20 years for the period 1650–1850. These are comparable to estimates from oak forests in Ohio (Sutherland, 1997; McCarthy et al., 2001) and limited evidence from New Jersey (Buell et al., 1954). More work on local fire-scar evidence is urgently needed while living or recently dead trees that germinated between 1600 and 1800 are still available.

Paleoecological evidence has the potential for clarifying presettlement fire frequencies, but currently the standards for relating fire frequency to charcoal abundance are being debated (Patterson and Backman, 1988; Clark and Royall, 1995b; Campbell and McAndrews, 1995). Studies in coastal Massachusetts have reported high charcoal–pollen ratios of 300–1000 on some sites (Patterson and Backman, 1988; Fuller et al., 1998; Parshall et al., 2003). As might be expected, charcoal influx is sometimes higher after the onset of European contact and settlement, reflecting the widespread use of fire in land-clearing activities (Perley, 1891). Yet charcoal influx at many oak–pine sites showed relatively little change after the point of European colonization (Watts, 1979; Maenza-Gmelch, 1997; Patterson and Backman, 1988; Fuller et al., 1998; Parshall et al., 2003), a trend also seen in fire scar studies (Dey and Guyette, 2000; Shumway et al., 2001).

A notable feature of the pollen record at many sites in southern coastal New England is the low percentage (1–4%) of the total pollen count contributed by grass, shrub, and herbaceous pollen. This suggests that open grasslands and heathlands were probably at most local occurrences in presettlement times (Motzkin and Foster, 2002; Foster and Motzkin, 2003). The implications of pollen data for the extent of open woodlands is currently less clear. Janowiak (1987) reported only 7% non-arboreal pollen from a varved lake in a region of southern Wisconsin that was heavily dominated by oak savanna in presettlement times (see also Winkler, 1985). Detailed land surveys taken at about the same time suggest tree densities of <50 trees/ha (Tans, 1976; Bollinger et al., 2003). Further studies may be needed to determine if non-arboreal pollen counts can provide reliable distinctions between open oak woodlands and closed-canopy forests.

4.3. Forest age structure on the presettlement landscape

Oak forests of the mid-Atlantic and southern New England uplands probably ranked second to pine–oak barrens in frequency of severe disturbances and the proportion of habitat suitable for early successional species. Recurrence intervals of 85–380 years for catastrophic wind damage in the southern half of New England imply that most stands would have been heavily dominated by the post-hurricane age cohort. Relatively few stands on exposed sites would have been old-growth stands except toward the end of the time interval between consecutive hurricanes (cf. Henry and Swan, 1974). Multi-cohort stands with a component of mature and old trees would have been common on protected sites and on some exposed sites, occupying roughly 25–40% of the landscape (cf. Foster, 1988b; Foster and Boose, 1992; Boose et al., 2001; Orwig et al., 2001). Calculating the mean proportion of the landscape in young forest habitat in this region, however, would not be very meaningful because of the erratic temporal fluctuations. The proportion of landscape in seedling–sapling habitat could vary from 40 to 50% immediately after a severe hurricane to probably <3% once the post-disturbance cohort had moved into the pole and mature age classes.

For oak forests in coastal sites and major river valleys, a regime of low- to moderate-intensity fires set mostly by Native Americans may have been superimposed upon this regime of severe wind disturbance. There is, however, currently no direct quantitative evidence that would permit numerical estimates of how much of the region may have been fire-influenced and dominated by open oak woodlands.

Oak forests distant from the influences of F2 hurricanes may have had a much different disturbance regime. Limited fire-scar evidence (Buell et al., 1954; Shumway et al., 2001) and the low frequency of shade-tolerant species cited in many presettlement land surveys suggest that fire frequency may also have been high in interior locations. Catastrophic wind disturbance was probably infrequent. Modern ecological studies suggest a natural disturbance rate of about 0.6–1% per year, mostly as small gaps within a matrix of old-growth forest (Runkle, 1990). So the proportion of the landscape in young forest stands (1–15 years) created by windthrow in the interior sections was probably low, perhaps similar to the prevailing rates in northern hardwood forests (1–3%; cf. Table 1).

5. Northern hardwood forests

Northern hardwood forests, dominated by American beech, sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), occur in a climatic zone with a frost-free period of 120–150 days (Lull, 1968). In New England and northern New York, northern hardwoods are found on spodosols of the New England Upland physiographic province and at moderate elevations along the Appalachian mountain chain. Northern hardwoods also dominate the Allegeheny Plateau of southern New York and northern Pennsylvania, found primarily on inceptisols. Extensive tracts of beech–maple forest also occurred in presettlement times on alfisols of the Lake Ontario plain in western New York (Seischab, 1990).

Northern hardwoods are usually considered to be late-successional forests, but the dominant species persist well after catastrophic windthrow because of the resilience of advance regeneration. In presettlement times, beech was often the major dominant, usually averaging 30% or more of the witness trees (McIntosh, 1962; Siccama, 1971; Cogbill, 2000). Eastern hemlock (*Tsuga canadensis*), a shade-tolerant conifer, was often intermixed with hardwoods but was somewhat patchy in occurrence, averaging 12–20% of the witness trees. White pine, an early to mid-successional species, locally dominated sites after catastrophic disturbance, especially fire. Across the region, white pine was a relatively minor species, averaging 1–5% of the witness trees, but made up to 20% of the forest in some of the major river valleys. It was most commonly dominant on sandy river terraces (Siccama, 1971; Whitney, 1994; Cogbill, 2000).

5.1. Windstorms and ice storms

Windstorms are probably the major natural cause of catastrophic disturbance in the northern hardwood region. These include hurricanes and other cyclonic storms, thunderstorms, derechos, and tornadoes. Hurricanes are probably the dominant type of destructive windstorm in much of southern and central New England. In the Pisgah State Park of southern New Hampshire, about 25% of the landscape was severely disturbed and 50% moderately disturbed in the 1938 storm (Foster, 1988a). In 1950, a great cyclonic storm originating over the Appalachian Mountains passed across the Adirondack Mountains of New York and caused moderate to severe disturbance on a district of about 160,000 ha (Jenkins, 1995).

Derechos are fast-moving convective storms that potentially may have more impact in inland regions. Derechos can cover a wide area and produce several episodes of violent downdrafts with speeds exceeding 160 km h^{-1}. Individual downbursts can range from 4 to 40 km in length (Jenkins, 1995). Derechos and downbursts are common in the midwestern US but have been less frequently reported in the northeast. However, a derecho crossed the Adirondack Mountains in 1995, causing a mosaic of lightly and heavily disturbed patches across a region of approximately 364,000 ha. The total area on which >30% of trees were killed was about 36,000 ha (Jenkins, 1995). A great windfall in 1845 that extended from western New York to western Vermont may also have been caused by a derecho (Jenkins, 1995). Similar thunderstorm downbursts may be responsible for many of the large windfalls reported in 18th and 19th century land survey records (Canham and Loucks, 1984).

Little evidence is available on the size range of blowdowns in northeastern northern hardwoods. Probably the most detailed map was prepared by Jenkins (1995) for the Adirondack blowdown based on low-altitude aerial photos of one of the most heavily impacted areas (Fig. 4). We digitized this map to produce estimated patch size distributions (Fig. 5). Individual patches ranged from <1 to 700 ha. As in the analysis of the 1938 hurricane by Foster and Boose (1992), most of the patches in the Adirondack blowdown are small. Several large patches account for much of the blowdown area; more than 40% of the total blowdown area is in patches >100 ha (Fig. 5). Such large patches may provide important habitat for early successional wildlife species that are area-sensitive.

Of the 36,000 ha of moderate and severe damage in the 1995 Adirondack blowdown, 29,000 ha were classified as having moderate damage (30–60% of trees toppled) and 7000 ha had severe damage (>60% of trees down; Jenkins, 1995). As in the 1938 hurricane, the pattern of damage was heavily influenced by topographic exposure. In the portion of the blowdown shown in Fig. 4, the storm hit windward west and northwest slopes and ridges most heavily. This study, along with those by Hough and Forbes (1943), Foster (1988a), Engstrom and Mann (1991), and Mann et al. (1994) demonstrate that ridgetops and upper slopes generally have higher than average disturbance rates and are potentially more dependable sources of suitable habitat for early successional species.

Ice storms can also cause damage over extensive areas. The ice storm of 1998 affected >6.9 million ha of northern hardwood and spruce–hardwood forest in northern New England and New York. Effects at the stand level were highly variable, reflecting complex interactions of meteorological conditions, stand composition and structure, and topography. Surveys of the affected areas revealed that >50% of the sampled trees had no crown loss whereas more than 21% had heavy (50–79%) or severe (80–100%) crown loss. Only the 12% with severe loss were categorized as unlikely to survive (Miller-Weeks et al., 1999). This suggests that although regionwide volume and financial losses were considerable, the 1998 ice storm was not typically a stand-replacing event. Given that this was one of the most intense and severe ice storms on record for the region, it seems reasonable to assume that ice storms

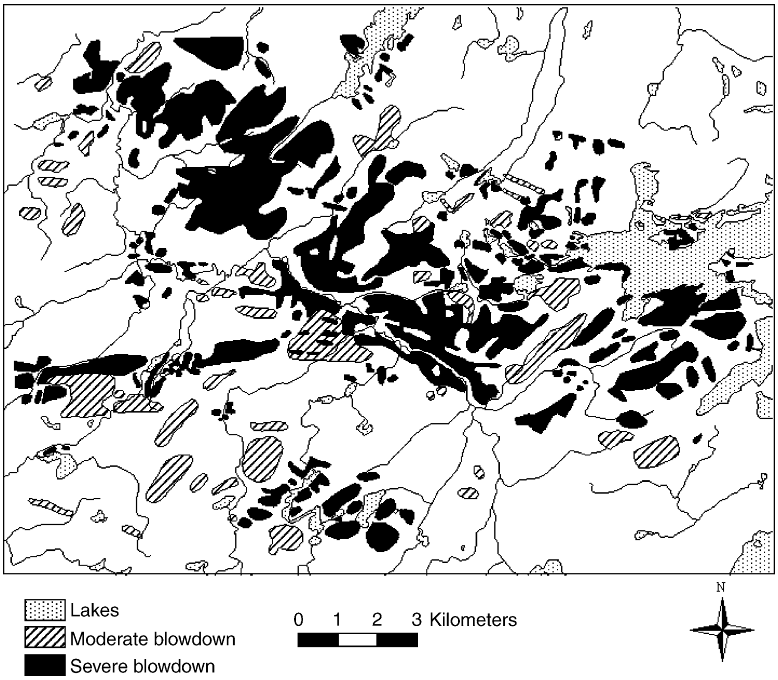

Fig. 4. Map of blowdown patches caused by the 1995 derecho in the Adirondack Mountains, New York, based on low-altitude aerial photos and reconnaissance in the region of heaviest damage (after Jenkins, 1995; reproduced with permission of the Wildlife Conservation Society).

are generally an agent of patch dynamics within forest stands (see also Seischab et al., 1993).

Aside from these isolated case studies, there has been little effort to systematically quantify annual disturbance rates by recent windstorms and ice storms. The best estimates of natural disturbance rates at the landscape scale are therefore still the presettlement land survey records of the 18th and 19th centuries (Cogbill, 2000). These records suggest that in spite of some of the spectacular storms in the historical record, the average rotation period for catastrophic storm disturbance is rather long for areas not normally subjected to F2 Atlantic hurricanes. Studies of land survey records of 1763–1810 in New Hampshire, Vermont, New York, and Pennsylvania indicate that large patches of standing dead and fallen timber covered only 0.2–1.5% of the landscape (Seischab, 1990; Whitney, 1990; Seischab and Orwig, 1991; Marks et al., 1992; Cogbill, 2000). If surveyors recorded storm-damaged areas up to 15 years old, this translates into mean rotation periods of 1000–7500 years. These 15-year storm disturbance rates are comparable to rates of 0.7–3.5% reported in northern hardwood forests of the Great Lakes region based on mid-19th century survey records (Canham and Loucks, 1984; Whitney, 1986; Zhang et al., 1999), and from reconstructive field studies of old-growth stands for the period of 1850–1980 (Frelich and Lorimer, 1991b; Frelich and Graumlich, 1994; Ziegler, 1999). This concurrence of evidence from different methods over a vast region and over a long period of time suggests that these are probably reasonable estimates of 18th and 19th century storm-disturbance rates. In northern hardwood regions under the influence of Atlantic hurricanes, the average interval between stand-replacement events was much shorter, ranging from 150 to 380 years on exposed sites (Boose et al., 2001).

5.2. Fire regimes

Lightning fires are uncommon in the northern hardwood region, usually making up less than 3% of all fires (Jenkins, 1995). Northern hardwood forests are generally less susceptible to intense fires than most other forest types in the region. In contrast to the loose and porous fuel beds of oak and pine, leaves of maple

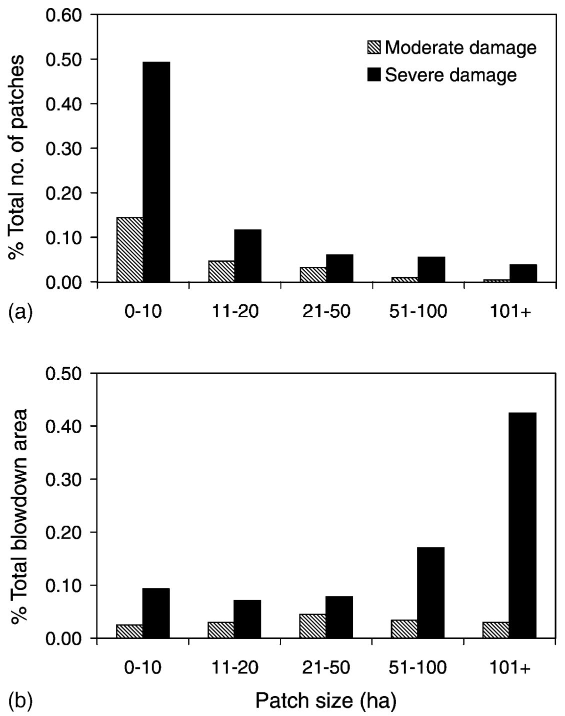

Fig. 5. Patch size frequency (a) and proportion of total blowdown area in different patch sizes (b) based on the map of the 1995 Adirondack blowdown in Fig. 4.

and birch are thin and easily matted down by rain and snow. The mesic soil conditions of many northern hardwood sites also hinder fire spread. However, fire scars and modern fire records show that surface fires can spread over large areas under certain conditions. For example, in October 2000, a lightning-ignited surface fire, fanned by strong northwest winds, spread over more than 560 ha of mature sugar maple forest in the Porcupine Mountains, Michigan in three days, despite prompt suppression attempts (Anon., 2000). Early surveyors in northern Maine recorded several consecutive miles of "hardwood killed by fire" during the dry year of 1825 (Lorimer, 1977). But generally, intense fires are common only in areas of heavy down fuel accumulations such as logging slash and blowdowns. Ayres (1909) noted that nearly all fires in the White Mountains of New Hampshire originated on cutover land, and the boundaries of the fires closely corresponded to the recently logged areas, as did fires in the Adirondack Mountains and northern Maine at about the same time (Spring, 1904; Jenkins, 1995).

Studies of old-growth stands confirm on-site evidence of both surface fires and stand-replacing fires, although most reported cases have been in pine–hemlock stands (Lutz, 1930; Hough and Forbes, 1943; Foster, 1988a; Mann et al., 1994; Abrams and Orwig, 1996). In a pine–hemlock forest on exposed knobs and escarpments in the Green Mountains of Vermont, Mann et al. (1994) documented an 18-year mean fire interval between 1504 and 1851, including three fires that led to some new canopy recruitment. Lutz (1930) also reported abundant charcoal fragments in an old-growth hemlock–beech forest about 8 km from the Allegheny River in Pennsylvania. A field examination of stumps adjacent to this stand suggested as many as 40 fire scar dates (not cross-dated) spanning the period from 1725 to 1925. At least five major surface fires occurred over the 200-year period, two of them during the presettlement era.

Quantitative evidence on the frequency of stand-replacing fires is available from three independent methods, all suggesting rather long return intervals. Presettlement land survey records indicate that the proportion of survey lines intercepted by burned lands was very low, probably 0.5% or less over much of northern New England, New York, and the western Allegheny Plateau of Pennsylvania (Siccama, 1971; Seischab, 1990; Seischab and Orwig, 1991; Marks et al., 1992; Cogbill, 2000). This would result in rotation periods of >3000 years. Burned windfalls, however, were probably one of the major successional pathways that led to dominance of stands by white pine (Hough and Forbes, 1943; Foster, 1988a; Abrams and Orwig, 1996) and birch–aspen. Burned lands and white pine stands were most common along the major river corridors (Cogbill, 2000), probably because of more intense human activity in those areas.

Fahey and Reiners (1981) used 20th century historical records to derive independent estimates of natural fire frequency in Maine and New Hampshire. Reasoning that the most accurate records of lightning fire frequency are probably the more recent ones (because of improved detection) but that the best estimates of mean fire size are those in the pre-fire suppression era, they multiplied mean fire size from 1903 to 1910 by recent estimates of mean annual frequency of lightning fires. This method yielded an estimate of 1070 years for a natural fire rotation in northern hardwoods.

Paleoecological evidence also suggests long fire intervals between severe fires in northern hardwoods. Using a new thin section technique on sediment cores, Clark and Royall (1996) reported that the sedimentary record showed low rates of charcoal accumulation but no clear evidence of local fires from two northern hardwood sites in Maine. In a forest hollow dominated by hemlock in central Massachusetts, Foster and Zebryk (1993) identified six charcoal horizons from the past 8000 years, but only one of these dated to the past 3000 years. Other paleoecological studies of hemlock–hardwood stands in central New England have found either little evidence of fire (Patterson and Backman, 1988; McLachlan et al., 2000) or relatively long fire intervals of about 600 years (Schoonmaker, 1992).

5.3. Forest age structure on the presettlement landscape

Northern hardwoods on the interior uplands probably had the lowest frequency of stand-replacing disturbances among the major forest types in the northeast. In the interior Allegheny Plateau and Appalachian Mountain regions, most lines of evidence suggest average rotation periods of 1000–3000 years for catastrophic windthrow and similar rotation periods for stand-replacing fires. The pooled disturbance rates for wind and fire result in an overall rotation period for catastrophic disturbance of 500–1500 years. The proportion of seedling–sapling habitat (1–15 years old) under these disturbance regimes ranges from 1 to 3%. Stands 15–30 years old would make up an additional 1–3% of the landscape (Table 1).

Because of the long rotation periods, the slope of the negative exponential curve is very shallow, and so estimates of young and mature forest based on the uniform and negative exponential models are quite similar. For example, with an overall rotation period of 500 years, the proportion of the landscape in stands up to 100 years of age is 20% with the uniform model and 18% with the negative exponential model. The effects of underlying model assumptions on the total amount of old-growth forest are also slight for overall rotation periods longer than 500 years. The estimated proportion of the landscape in old-growth forest (>150 years old) is 70–89% depending upon rotation period and model form.

The presettlement age distributions in Table 1 suggest ratios of uneven-aged to even-aged stands ranging from about 3:1 with a 500-year rotation period to 8:1 for a rotation period of 1365 years. Among mature and old stands only, the ratio of uneven-aged to even-aged ranged from 5:1 to 14:1. Field verification of these ratios is difficult because of the rarity of old-growth stands, but a predominance of uneven-aged stands is evident from stand age data on inland sites obtained by Hough and Forbes (1943), Leak (1975), Chokkalingam (1998), and Ziegler (1999). The 1365-year rotation period (2500 years for wind, 3000 years for fire) results in an overall landscape age distribution that is quite similar to an age distribution reconstructed from field data and simulations for large natural landscapes of northern hardwood forest in Michigan (Frelich and Lorimer, 1991a).

In spite of the low rates of stand-replacing disturbance, disturbances of moderate intensity were much more common and probably provided suitable habitat for some early successional species (cf. Greenberg and Lanham, 2001). In the 1995 Adirondack windstorm, the zone of moderate disturbance was four times as large as the zone of catastrophic disturbance. Likewise, a notable feature of many old-growth hemlock–hardwood stands is the dominance by 2 or 3 age cohorts, suggesting episodes of partial canopy removal at intervals of 60–400 years (Hough and Forbes, 1943; Frelich and Lorimer, 1991b; Chokkalingam, 1998; Ziegler, 1999). These gaps are often rather small (<300 m^2), but given the point recurrence intervals suggested by the old-growth stands, moderate disturbances could potentially affect an additional 3–25% of the landscape over a 15-year period.

6. Spruce–northern hardwood forests

Northern hardwood forests with a substantial admixture of spruce (*Picea* spp.) and other conifers are common on a variety of habitats in northern New England and New York. Spruce–hardwood forests are best discussed separately from other northern hardwood forests because of differences in both physical environment and disturbance regime. Spruce and fir (*Abies balsamea*) in particular are much more vulnerable to windthrow, insect epidemics, and crown fires than most of the associated species.

Spruce–northern hardwood forests occur mostly on spodosols and in a climatic zone with a frost-free period of 90–120 days (Lull, 1968). Four distinct habitats are often recognized, each of which probably has a different disturbance regime: (1) spruce swamps, (2) "spruce flats" on relatively level and often stony soils near lakes and streams; (3) mixed forests of spruce and northern hardwood species on the better soils of lower slopes and low ridges, and (4) the "spruce slope" type on high mountain slopes or on ridges with thin, rocky soil. The proportion of spruce in the forest averaged about 15–20% across the region prior to settlement, but often reached 60–80% on the high slopes. Other conifers such as balsam fir, hemlock, northern white cedar (*Thuja occidentalis*), larch (*Larix laricina*), and eastern white pine collectively averaged 12–40% of the trees in different habitats and in different geographic regions (Siccama, 1971; Lorimer, 1977; Cogbill, 2000). Paleoecological studies indicate that for much of the mid-Holocene, northern hardwood species largely dominated the region. The invasion of spruce is a relatively recent phenomenon of the last 2000 years, probably in response to climatic cooling (Anderson et al., 1986; Schauffler and Jacobson, 2002).

6.1. Windstorms

Spruce and fir are susceptible to windthrow because of their shallow root systems and the tendency to predominate in swamps, on upland sites with thin and stony soils, and on mountain slopes exposed to severe winds. Graves (1899) noted that on these extreme habitats, windfall was common and that trees were usually blown down before reaching (biological) maturity. As a consequence, pure stands of spruce in the Adirondacks were usually composed of comparatively young trees. Graves (1899) also indicated a typical average diameter of 33 cm for canopy trees in spruce swamps (equivalent to an average age of 180 years), and noted that spruce forests in the swamps, flats, and high mountain slopes facing the prevailing winds were often relatively even aged. In contrast, extensive tracts of mixed spruce–northern hardwoods were seldom destroyed by natural forces, but individual trees were continually dying and being replaced, resulting in a forest that included trees of all sizes and ages (Graves, 1899). This overall assessment was shared by Hawley and Hawes (1912) and Murphy (1917).

As in the northern hardwood region to the south, the spruce–hardwood region is subjected occasionally to large storms capable of causing windthrow over extensive areas. Outside of the Adirondacks, the largest known windstorm documented in reasonable detail occurred about 1795 north of the Piscataquis River in northern Maine (Morse, 1819; Lorimer, 1977). Descriptions by land surveyors working in the area in 1801 suggested a typically heterogeneous patchwork of heavily and lightly disturbed stands. The full extent of the storm damage was difficult to ascertain because portions of the region were surveyed at different times, and subsequent fires burned much of the tract in 1803, 1811, and 1825. But references to extensive windfalls and burned windfalls that seemed to be connected with the 1795 storm occurred in a zone about 72 km from west to east and about 20 km from south to north, nearly all in the Piscataquis Valley. The overall boundaries of the region known to have had numerous windfalls encompassed 144,000 ha, about 40% as large as the zone impacted by the 1995 Adirondack derecho. The total area of blowdown within this zone was not known, but based on the available descriptions, severity seems comparable to the 1995 Adirondack storm. Another large storm occurred in northern Maine in November 1871. According to Hough (1882), a snowstorm in that month was followed by a severe gale that blew down many trees and extended hundreds of miles in Maine and New Brunswick. In recent times, one of the more notable storms, albeit of much smaller magnitude, was a blowdown of about 2500 ha in northcentral Maine in 1974 (Kolman, 1978).

Presettlement land surveys provide the best evidence of disturbance rates and rotation periods at the landscape level. Windfalls and burned areas recorded by surveyors in New Hampshire, Vermont, and northern New York occupied about 0.5% of the landscape, and suggest long rotation periods. In northeastern and northcentral Maine, surveyed between 1793 and 1827, recent windfalls occupied somewhat less than 2.6% of the landscape (Lorimer, 1977). This suggests rotation periods for severe windthrow on the entire landscape of 575–1150 years, depending upon whether a 15- or 30-year time span is assumed. There was clearly a difference in windthrow frequency, however, between spruce-dominated forests in lowlands and mixed spruce–hardwood forests on the uplands, with most of the blowdown area located in conifer-dominated forests in swamps and on stony flats. If these habitats are analyzed separately, the rotation period (15-year time window) for severe windthrow in the mixed spruce–hardwood forests and northern hardwood dominated forests on the better soils is 2585 years, while the rotation period for conifer forests on lowland sites and on poor, rocky soils is only 290 years.

6.2. Insect epidemics

Many insects are capable of killing trees in spruce–northern hardwood forests. Only a few native insects, however, are known to cause widespread mortality. These include the spruce budworm (*Choristoneura fumiferana*), spruce beetle (*Dendroctonus rufipennis*), and larch sawfly (*Pristiphora erichsonii*). Because these insects are reasonably host-specific, in mixed forests they normally kill scattered trees or small groups. However, in stands heavily dominated by spruce, fir, or larch, they can kill most of the stand. Epidemics can be triggered by an abundance of susceptible trees, weather patterns favorable for buildup of insect populations, and abiotic factors that weaken the host trees. Stands with a high percentage of mature balsam fir are particularly vulnerable to spruce budworm. Stands of mature spruce weakened by windthrow or logging are likewise susceptible to spruce beetle outbreaks (Schmid and Beckwith, 1975).

Two large-scale epidemics of spruce budworm have occurred in recent times in northern Maine, including outbreaks that caused very heavy mortality in 1913–1919 and 1972–1986. An earlier epidemic of 1876–1879 reportedly killed one billion board-feet of spruce, about half of the merchantable spruce volume, in the Allagash River region of northwestern Maine (Hough, 1882). The 20th century outbreaks are believed to have been exacerbated by decades of selective logging of the more valuable red spruce (*Picea rubens*), which led to unusual dominance by more susceptible balsam fir (Zon, 1914; Swaine and Craighead, 1924; Seymour, 1992). Nevertheless, there are at least two credible reports of major insect outbreaks in spruce forests that occurred too early to have been triggered by human activities. Packard (1881) cited two independent reports of an insect outbreak in 1818 that killed almost every spruce west of the Penobscot River. Hopkins (1901) cited widespread spruce mortality from 1844 to 1859 in two New York counties in the Adirondack Mountains. The geographic extent of these early outbreaks is not well known, however, and different writers attributed dieback to various causes including spruce beetle, spruce budworm, drought, and cold weather. Hough (1882) suggested that the dieback of 1876–1879 was caused by insects and triggered as a result of trees weakened by the extensive windstorm of November 1871.

Because insect-killed conifers are easily windthrown and are highly flammable, these various disturbances do not act independently. It is therefore possible that some areas of windthrow and burned land in the early land surveys might have been first subjected to insect outbreaks. At the time of the 1793–1827 land surveys in northeastern Maine, however, only four small areas were explicitly described as having "much dead and down spruce" (Lorimer, 1977).

6.3. Fire regimes in spruce–hardwood forests

Natural fire frequency in spruce–hardwood forests is a difficult and complex topic. There is no question that large and severe fires do occur in this forest type but evidence on the frequency and rotation periods of such fires is difficult to interpret. There also may be important regional differences. Siccama (1971) found no reports of burned land in the presettlement land surveys of 1783–1787 in the northern half of Vermont, and Cogbill's (2000) analysis of a much larger portion of the northeast also showed burned lands to be uncommon. But Maine has had a long history of large and intense fires (Hawley and Hawes, 1912; Coolidge, 1963).

Mature and old-growth forests of spruce and northern hardwoods do not burn readily. Hawley and Hawes (1912) pointed out that most fires occur in areas where trees were harvested, and uncut stands were usually resistant to fires. However, some large fires in mature stands have occurred in the past two centuries (Lorimer, 1977, 1980).

Prior to European settlement, abundant windfalls provided similar fuel conditions to those of cutover lands and some of these did burn (e.g., the 1795 blowdown in northern Maine). However, ignition probabilities of blowdowns are not well known, and some large historic blowdowns did not catch fire (Jenkins, 1995). The overall frequency of lightning fires in Maine is low (0.45–0.81 lightning fires per 1000 km^2 per year; Fobes, 1944; Fahey and Reiners, 1981), similar to lightning fire frequency elsewhere in the Northeast (Schroeder and Buck, 1970). According to survey records (Siccama, 1971; Lorimer, 1977; Cogbill, 2000), early successional and post-fire species (e.g., *Betula papyrifera*, *Populus tremuloides*, *Prunus pensylvanica*, *P. strobus*) made up only a small proportion of the presettlement forest in northern New England. This evidence is consistent with comments by foresters familiar with areas of old-growth forest in the late 19th century. Dana (1930) stated that white birch and aspen were poorly represented in the original forest. Of the intolerant birches (*B. papyrifera* and *B. populifolia*), Cary (1896) remarked that ''neither, of course, was a large element in the natural forest, but they have come in largely on burnt and cleared land.'' These pioneer species usually dominate stand-replacement burns on upland sites, although shade-tolerant species such as spruce and beech are often present and are sometimes locally dominant (Dana, 1909; Ayres, 1909; Lorimer, 1980; Patterson et al., 1983).

Shortly before settlement, recently burned lands (1–15 years old) occupied 3.9% of the landscape in northeastern Maine, mostly from two very large fires of 10,000 ha and 32,000 ha that occurred in 1825. An additional 5.1% of the landscape was recorded as old burn, mostly from the 80,000 ha fire of 1803 (Lorimer, 1977). At the time of the 1825–1827 surveys, the 1803 burn was occupied by white birch and aspen. An additional 0.6% was occupied by pole-mature stands (probably up to 75 years old; cf. Cary, 1894b, 1896; Dana, 1909) in which white birch and aspen were listed among the dominant species. Interpretation of these data is complicated by the fact that the year 1825 was the worst fire year in the state's recorded history (Coolidge, 1963), and by the use of land-clearing fires by the first settlers from 1799 to 1825 (Loring, 1880). Overall, the amount of forest burned over a 75-year period suggests a fire rotation period of about 800 years. The amount of land burned only during the more recent 15-year period from 1811 to 1826 suggests a shorter rotation of 385 years, and use of a 30-year period from 1796 to 1826 would imply a rotation of about 330 years.

Fahey and Reiners' (1981) use of mean fire size in the early pre-suppression era (1903–1910), combined with modern data on lightning fire frequency, is the only other historical estimate of natural fire rotation periods. This approach suggested a fire rotation of 1240 years for spruce–fir forests in Maine, the longest for any of the major forest types. We examined the same data but made some different assumptions about fire potential in drought years to provide a sensitivity analysis. In most years, lightning fires account for only about 1.5% of the total burned area, but lightning fires contribute 17–21% of the burned area in some years (mean intervals of about 5 years; Fobes, 1944). We therefore applied these two different proportions to the early fire data from 1903 to 1915 in the Maine Forestry District, which at that time comprised about 3,846,150 ha of mostly spruce–hardwood forest (Coolidge, 1963). We assumed that lightning caused 20% of the total burned area in the three peak fire years of 1903, 1908, and 1911, and 1.5% in each of the other 10 years. This resulted in fire rotation periods (including slash fires and ground fires) of 1253 years for 1903–1910 and 1519 years for 1903–1915.

Analysis of sedimentary charcoal at three sites in northcentral and northeastern Maine also has suggested infrequent fires. Clark and Royall (1996) considered the size of charcoal particles and the concentration too low to indicate local fires in the past 1500 years near Conroy Lake, and Schauffler and Jacobson (2002) could find little evidence of fire over a period of 5000 years at the Big Reed Preserve. Anderson et al. (1986), however, found evidence of at least two major fires that occurred about 3500 and 1500 years ago at South Branch Pond. In the spruce–fir forests of coastal Maine, Schauffler and Jacobson (2002) found only small amounts and small-sized particles of charcoal, suggesting infrequent fire in those habitats for most of the Holocene.

As in the case of northern hardwoods, age-structure analysis of remnant old-growth spruce–hardwood stands provided limited verification for these estimates of disturbance frequency. Among 10 old-growth stands at the Big Reed Preserve in northcentral Maine and two stands in the White Mountains of New Hampshire, there was a strong predominance of uneven-aged or multi-aged stands and low importance values for pioneer species that commonly regenerate after fires (Leak, 1975; Moesswilde, 1995; Chokkalingam, 1998;

Chokkalingam and White, 2001). Data collected from 18 old-growth stands by early foresters also indicated a predominance of species and stands (about 60%) with relatively smooth, descending size distribution curves, even in the spruce slope type (Cary, 1894a, 1896; Hosmer, 1902; Chittenden, 1905). Size distributions are less conclusive evidence than direct examination of tree cores, but descending size distributions for individual species are usually characteristic of uneven-aged or multi-aged structures (cf. Leak, 1973, 1975; Moesswilde, 1995; Chokkalingam, 1998). These limited age and size distribution data appear consistent with broader generalizations about age structure in old-growth spruce–hardwood stands by early foresters. Hawley and Hawes (1912) stated that "the (spruce–hardwood) forest as a whole is composed of trees of all ages; it is thus an 'uneven-aged' or 'all-aged' forest. Exceptions to this character occur; for sometimes a part of the forest is found where the trees are all of one age over considerable area; i.e., an 'even-aged' forest. But such cases are in the minority."

6.4. Forest age structure on the presettlement landscape

Regional average rates of catastrophic disturbance in spruce–hardwood forests are rather difficult to verify because of the pronounced temporal and habitat-related variability. Tables 2 and 3 show estimated regional stand age distributions for rotation periods ranging from 575 to 1000 years for windthrow and 385–1200 years for fire. These correspond to overall rotation periods for stand-replacement events of 230–545 years. The proportion of seedling–sapling habitat (1–15 years) ranges from 2.7 to 6.5% depending upon the rotation period and model form. Stands 15–30 years old make up a similar proportion of the landscape. Stands 60–150 years old range from 13 to 39% and old-growth stands (>150 years old) from 35 to 76%.

The Maine land surveys enable a preliminary estimate of habitat-related variability, in this case the contrast between mixed spruce–hardwood forests on the better soils of lower slopes and low ridges and the conifer-dominated sites in swamps, stony flats, and steep, high-elevation sites (Lorimer, 1977 and Table 3). The pooled wind/fire rotation period of 606 years for mixed spruce–hardwood forests results in a landscape age distribution similar to northern hardwood forests elsewhere, with 2.4% in seedling–sapling habitat and 75–78% old growth. The conifer forests in swamps and on rocky sites, in contrast, had a pooled rotation period of only 210 years, giving a landscape with 7% seedling–sapling habitat and 29–39% old-growth forest.

Although the age distributions in Tables 2 and 3 vary widely, some of these may be more plausible than others based on other lines of evidence. The scenario in Table 2 with the shortest overall rotation period (375 years for fire, 575 years for wind, 230 years overall) implies that even-aged stands would occupy about 48% of the landscape, and that post-fire stands up to 75 years of age would have dominated about 18% of the landscape. Given the generally low representation of post-fire species in the presettlement forest, the predominance of uneven-aged stands described by early foresters, the predominance of uneven-aged structures among remnant old-growth stands, and the low levels of sedimentary charcoal, an average 230-year rotation may be too short for the region as a whole. However, it may lie within the historic range of variability and may even be a common disturbance frequency for some habitats and subregions. A 1000-year rotation period for severe windthrow and 1200 years for stand-replacing fire would result in about 24% of the landscape occupied by even-aged stands and 76% by uneven-aged stands, with 6% of the landscape in post-fire stands up to 75 years old. These figures seem more consistent with the currently available evidence. The best tentative estimates of the proportion of the landscape in seedling–sapling habitat (1–15 years old) thus lie between 2.5 and 4.5%, with a similar proportion between the ages of 15 and 30 years.

7. Conclusions

Natural disturbance regimes vary markedly across the northeastern US, being influenced primarily by geographic location, forest type, and local habitat conditions. In presettlement times, there seemed to be a gradient in the frequency of stand-replacing disturbances from coastal regions to interior zones. From Delaware to southern Maine, coastal regions often had the highest disturbance frequencies because of the large expanses of sandy pine–oak barrens near the coast, abundant populations of Native Americans, longer snow-free periods, and the influence of occasional destructive hurricanes. In situations where presettlement or early historic disturbance rates can be quantified, the average proportion of the landscape occupied by seedling–sapling habitat was probably only 1–3% in the northern hardwood forests of northern New England, New York, and Pennsylvania. However, seedling–sapling habitat may have occupied, on average, more than 10% of the landscape in some of the coastal pine–oak barrens. To this must be added an unknown proportion of the landscape in fire-influenced oak woodlands, some of which may have been rather "open" with less than full crown cover.

These regional averages do not reflect the high spatial variability that clearly occurred among specific habitats within a region or the high temporal variability that occurred within moderate-sized landscapes. In all forest regions, high ridgetops and sites with thin or rocky soil had a much higher than average frequency of blowdown and fire, and were probably the most dependable locations where early successional organisms might find suitable habitat. In the spruce–hardwood region, there is some evidence that seedling–sapling habitat may have occupied about 7% of the spruce swamp and spruce flat habitats, roughly twice the regional average. Also, within smaller subregions, the influence of occasional large-scale catastrophic events such as the 1938 hurricane or the 1995 Adirondack windstorm could disrupt the existing age distribution of forest over sizable areas, leading to major but temporary regional irruptions of early successional wildlife populations. Range of variability in time and space are probably more important than averages, yet are even more difficult to quantify given our current state of knowledge.

The regional averages also do not reflect the very significant impact of moderate-severity disturbances that typically removed 30–60% of the overstory. Stand reconstruction studies as well as contemporary observations suggest that these disturbances were much more frequent, and hence much more influential, than catastrophic disturbances in determining the overall structure of stands and landscapes. Evidence presented by Greenberg (2001) and Greenberg and Lanham (2001) for the southern Appalachian Mountains suggested that moderate-sized gaps 0.1–1.2 ha (created by a hurricane) can be important in creating suitable habitat for some early successional birds and reptiles.

Systematic data from the federal network of Forest Inventory and Analysis plots indicate that the current average proportion of seedling–sapling habitat in the northeast is about 16%, ranging from 4% in Massachusetts to 25% in Maine (Trani et al., 2001). If the modern seedling–sapling category (defined as young stands with predominant tree diameters <12.7 cm) is comparable in age range to those of recent blowdowns and burned areas cited by early surveyors, these data suggest that the current proportion of seedling–sapling habitat is probably similar to presettlement levels in some areas but higher or lower in others. For example, the current proportions of seedling–sapling habitat of 4–5% in Massachusetts and Connecticut are only moderately higher than presettlement estimates for the interior northern hardwood region. The current estimates of 9–25% for the northern New England states are probably several times higher than presettlement levels, even given the most generous estimates for the role of windthrow and fire in the spruce–hardwood region (see also Seymour et al., 2002). However, it is possible that the current estimates of 10–18% for the mid-Atlantic states may be comparable to (or possibly lower than) presettlement levels if fire was as widespread in the coastal regions as suggested by historical and fire-scar evidence, and if the pine barrens had presettlement fire rotations of less than 150 years. Because the "natural" proportion of the landscape in young forest habitat seems to be low in some regions, managers should be aware that restoring natural conditions could have unfavorable effects on many early successional species that may already be declining for various other reasons. Thus the "natural range of variability" concept may have some serious drawbacks in guiding conservation policy if it were to be implemented mechanically across the entire region (Litvaitis, 2003).

It is not yet clear if forest management practices that increase the amount of seedling–sapling habitat will be sufficient to reverse the declining trends of some early successional species. Many of the threatened and watch-list species cited by Hunter et al. (2001) are primarily grassland, heathland, and marshland specialists that make some use of young or open forest habitats. About 70% of grassland and shrubland birds have been undergoing long-term declines, for which habitat loss and human development patterns are clearly major causes (Hunter et al., 2001; Litvaitis, 2003).

Fewer species with distributions centered in the northern hardwood or spruce–hardwood regions have downward population trends, yet more than 40% of the species in those regions may be experiencing significant declines (Franzreb and Rosenberg, 1997; Hunter et al., 2001). Some of these cases may represent a readjustment of populations to habitat levels similar to those in presettlement times, whereas species with more serious declines (e.g., wood thrush (*Hylocichla mustelina*) and golden-winged warbler (*Vermivora chrysoptera*)) may be affected by other threats, including decline in quality of forest habitats, threats on the tropical wintering grounds, modern migration hazards, and loss of habitat to human development (DeGraaf and Miller, 1996; Franzreb and Rosenberg, 1997). To the extent possible, investigators should try to determine if increasing the amount of young forest habitat or modifying habitat structure is sufficient to reverse the population trends of species at risk.

Guidelines for restoring a more natural forest age structure in specific landscapes (e.g., national or state forests) may require more detailed investigations of historic disturbance regimes that are spatially linked to local habitat and site variation. Sampling, for example, could be stratified by habitats using existing ecological land classification systems (e.g., Smith, 1995; Gawler, 2000). All of the standard methods could be used in such investigations, including analysis of presettlement land surveys, stand history reconstructions of the larger old-growth remnants, paleoecological analysis of a network of small forest hollows, observations of contemporary natural disturbances, and computer simulation. Major progress toward interdisciplinary work of this type has been achieved at the Harvard Forest in Massachusetts (e.g., Fuller et al., 1998; Boose et al., 2001) and the Big Reed Forest Reserve in Maine (e.g., Moesswilde, 1995; Shauffler and Jacobson, 2002; Chokkalingam and White, 2001). Further interdisciplinary work of this type would be useful in those and other areas to provide some of the site-specific information needed by land managers as an aid in devising long-range management plans.

Acknowledgements

We thank David Foster, Bill Patterson, John Livaitis, and an anonymous reviewer for helpful suggestions on the paper. We would also like to thank David Foster, Bob Seymour, Charlie Cogbill, Bill Patterson, and the many others with whom we have had stimulating discussions over the years about disturbance dynamics of northeastern forests. The authors received support during the writing of this paper from the School of Natural Resources, University of Wisconsin-Madison, Maine Agricultural and Forest Experiment Station, and grants from the McIntire-Stennis Cooperative Forest Research Program and the Ecosystem Research Program of The Nature Conservancy.

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