

Natural disturbance in an old-growth landscape of northern Maine, USA

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Summary

1. Disturbance histories derived from old-growth forest remnants in Europe and eastern North America have shaped many of our current theories of forest dynamics and succession. Yet the small size typical of these remnants suggests they might not capture the full range of variability that may emerge at larger scales.

2. We investigated the frequency and severity of natural disturbance in a 2000-ha old-growth landscape (Big Reed Forest Reserve) in northern Maine, USA. Given its size, the Reserve provides an ideal opportunity to study, at multiple scales, natural forest processes in a region that has otherwise been dramatically altered by human activities. Using dendrochronological methods, we reconstructed disturbance histories for 37 randomly located plots stratified by five forest types (hardwood forests, mixed woods forests, red spruce forests, northern white-cedar seepage forests and northern white-cedar swamps).

3. We found no evidence of stand replacing disturbance on any plot during the last 120–280 years (depending on plot). The overall mean disturbance rate was 9.6% canopy loss per decade (median 6.5%, maximum 55%, plots pooled), yet the distribution was strongly skewed toward the lower rates.

4. We found little differences in disturbance rates between forest types, save a slightly lower rate in the northern white-cedar swamps. However, if we ignore forest-type classifications, we see that disturbance rates are clearly influenced by gradients in the relative abundance of component tree species, owing to species' relative susceptibilities to particular disturbance agents.

5. *Synthesis.* Relatively low rates of canopy disturbance allow the accrual of shade-tolerant saplings. The abundance of this advance regeneration, coupled with the absence of stand-replacing disturbance, has maintained canopy dominance by shade-tolerant species in all plots, all forest types and throughout the entire landscape. Disturbance histories from individual plots coalesce to form a picture of a landscape in which pulses of moderate-severity disturbance are interposed upon a background of scattered small-scale canopy gaps. The landscape-level mosaic resulting from this disturbance regime consists of patches in various stages of structural development, not various stages of compositional succession.

Key-words: advance regeneration, canopy gaps, dendrochronology, growth releases, late successional forests, shade tolerance, spruce budworm, stand dynamics, succession

Introduction

Ecologists have long recognized the role of natural disturbance in regulating forest structure, composition and processes at scales ranging from small patches to large landscapes (Pickett & White 1985; Turner 1987). The importance of natural disturbance concepts to both applied and theoretical ecology

can hardly be overstated. As a consequence, characterizing historic disturbance regimes for a given forest type or region has been a major research endeavour (e.g. Heinselman 1973; Zackrisson 1977; Frelich & Lorimer 1991; Bergeron 2000). Notably, many characterizations of historic disturbance regimes have been derived from old-growth forests, which provide a long-term record relatively uninfluenced by human activities.

Old-growth forests, however, are rather uncommon in much of the northern temperate region, owing to centuries of forest harvesting and conversion. In Europe and eastern North America, most of the remaining old growth is found in

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small isolated stands that escaped harvest simply because they occur on steep slopes, at high elevations, or are otherwise inaccessible (Peterken 1996; Cogbill 2000). As such, they may not be representative of natural forests that formerly covered the surrounding landscapes (Lorimer & White 2003). Yet disturbance histories derived from such stands have shaped many of our current theories of forest stand dynamics and succession. Even scarcer in these regions are old-growth landscapes, that is, thousands of hectares of contiguous forest that have escaped harvest.

In New England, USA, only one such old-growth landscape remains, namely the Big Reed Forest Reserve (approximately 2000 ha) of northern interior Maine. It provides an extraordinary opportunity to study, at multiple scales, the natural forest composition and processes in a region that has otherwise been dramatically altered by humans during the past century or centuries. Unlike small isolated stands that may be unrepresentative, the Reserve clearly represents the larger landscape: it supports forest types, soils, elevation ranges and topographic settings typical of northern Maine and much of New England. As such, it allows us to determine if inferences on natural disturbance drawn from isolated old-growth stands in this region (e.g. Henry & Swan 1974; Fraver & White 2005a) can be supported by landscape-level analyses. Because the Reserve supports a number of forest types, it also allows us to determine if rates and patterns of natural disturbance differ between forest types within a landscape. Such differences could easily exist, given host-specific disturbance agents, species-specific susceptibility to windthrow and the link between topographic position and forest type.

A number of methods are available for reconstructing the history of past disturbances (e.g. historical records, early land surveys, paleoecology and dendroecology), each having strengths and weaknesses with regard to spatial and temporal resolution. Inventories, such as the Public Land Surveys conducted in the US Lake States in the mid-1800s, provide important estimates of major disturbances throughout a large region (Schulte & Mladenoff 2005), but they do so at a rather coarse scale. Conversely, methods of dendrochronology can provide high spatial and temporal resolution, yet because of the formidable effort required to process large numbers of samples, the majority of dendrochronological studies of canopy-gap disturbance have been restricted to small areas (e.g. Henry & Swan 1974; Fraver & White 2005a; Piovesan *et al.* 2005). To the best of our knowledge, Frelich & Lorimer (1991) provide the only dendrochronological study that has explicitly evaluated patterns of canopy-gap disturbance that emerge at the landscape level. Their study provides critical insights on rotation periods, spatial patterns of disturbance, and on agents that could only be derived from landscape-level analyses. The lack of such information from other regions has limited our understanding of landscape-level disturbance patterns in these regions, in particular those arising from low- to moderate-severity disturbances.

The Big Reed Forest Reserve is dominated by shade-tolerant, late-successional, relatively long-lived tree species, as were extensive areas of temperate forests in northeastern

North America prior to European settlement (Cogbill 2000; Mosseler *et al.* 2003). Yet a surprising richness of major natural disturbances are known to occur in this region: low-pressure frontal storms (Jenkins 1995), hurricanes (Boose *et al.* 2001), *Choristoneura fumiferana* Clem (eastern spruce budworm) outbreaks (Fraver *et al.* 2007), *Dendroctonus rufipennis* Kirby (spruce bark beetle) outbreaks (Packard 1881) and wildfire (Parshall & Foster 2002). The occurrence of these disturbances suggests a level of canopy removal and, in the case of wind and fire, soil exposure that would promote early successional tree species. It is not well-understood how these disturbance agents have interacted with the autecologies of regional tree species to maintain dominance by late-successional species throughout this landscape.

Our general objective was to reconstruct, using methods of dendrochronology, the frequency and severity of natural disturbances that have shaped this old-growth landscape over the past several hundred years. In addition, we addressed the following two specific objectives. First, determine if disturbance rates differed among forest types within this landscape. We hypothesized that red spruce forests would have disturbance rates higher than the remaining forest types, given the documented history of insect outbreaks, as well as this species' susceptibility to windthrow (Canham *et al.* 2001). Second, explain the dominance of shade-tolerant tree species throughout the Reserve given the known or inferred history of disturbance for this region. We hypothesized that these disturbances, despite their potentially stand-replacing impact, did not result in significant canopy removal, thereby allowing the persistence of late-successional species. We combine intensive and extensive sampling that provides information at the scales – from plot to forest type to landscape – appropriate for meeting these objectives.

Methods

STUDY AREA

We conducted this work in The Nature Conservancy's Big Reed Forest Reserve of northern Piscataquis County, Maine (centred at 46°20' N and 69°5' W). Precipitation is evenly distributed throughout the year, with an average of 1058 mm annually (Baron *et al.* 1980). Mean monthly temperatures range from –10.0 °C in January to 19.8 °C in July, with an annual mean of 5.3 °C (Baron *et al.* 1980). The topography of the Reserve is undulating, with elevations ranging from 317 to 575 m a.s.l. Historical records and field observations reveal minimal evidence of timber harvesting within the Reserve (Cogbill 1985; Widoff 1985), largely due to its isolation from major rivers for transporting logs, as well as its protection by various owners throughout the 20th century. Nevertheless, *Pinus strobus* L. (eastern white pine) may have been harvested from the Reserve, given the region-wide harvesting of this species in the late-1700s to mid-1800s. Its removal, however, would have had a very minor impact, given that *P. strobus* was uncommon and occurred as scattered individuals at that time (Westveld 1931; Lorimer 1977). Also, low-intensity harvesting of *Thuja occidentalis* L. (northern white-cedar) from scattered swamps (not sampled in this study) occurred in the early 1900s (Cogbill 1985).

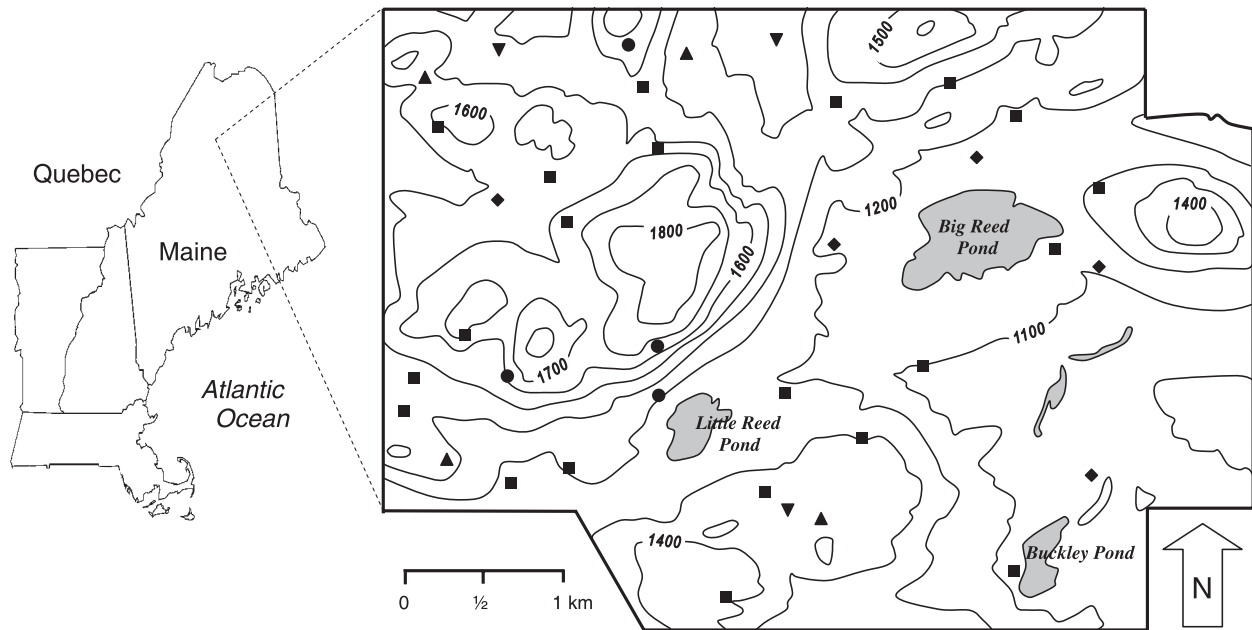


Fig. 1. Map of the Big Reed Forest Reserve in northern Maine showing location of the 37 plots (■, mixed woods; ◆, northern white-cedar seepage forest; ▲, red spruce forest; ▼, northern white-cedar swamp; ●, hardwood forest; none to scale). Elevations given in feet above sea level (1200 ft = 366 m, 1400 ft = 427 m, 1600 ft = 488 m and 1800 ft = 549 m).

The Reserve supports five primary forest types, listed here in order of decreasing areal extent within the Reserve. Forest-type nomenclature generally follows that of the Maine Natural Areas Program (1991). First, mixed hardwood-conifer forests (i.e. mixed woods) are dominated by *Acer saccharum* Marsh. (sugar maple), *Fagus grandifolia* Ehrh. (American beech), *Betula alleghaniensis* Britton (yellow birch), *Picea rubens* Sarg. (red spruce), and *Abies balsamea* (L.) Mill (balsam fir). This type is found on various landforms, typically on moderately well-drained soils. Second, northern white-cedar seepage forests are dominated by *T. occidentalis*, *P. rubens*, and *A. balsamea*; they occur on saturated gentle slopes with minerotrophic groundwater drainage. Third, red spruce forests are dominated by *P. rubens*; they occur in varied topographic settings, but typically on rocky substrates with shallow soil. Fourth, northern hardwood forests are dominated by *A. saccharum*, *F. grandifolia*, and *B. alleghaniensis*; they occur on mid or upper slopes with relatively rich soils. Fifth, northern white-cedar swamps are dominated by *T. occidentalis*; they occur on very poorly drained soils with a *Sphagnum* substrate.

Five of the six common species in the Reserve (*A. saccharum*, *F. grandifolia*, *P. rubens*, *A. balsamea*, *T. occidentalis*) are very shade tolerant; the sixth, *B. alleghaniensis*, is rated intermediate (Kneeshaw *et al.* 2006) to tolerant (Graves 1899). We agree more with Graves' rating, given the species' ability to sustain slow growth, presumably while positioned in the understorey, for decades before release (these data), as well as the prevalence of multiple episodes of suppression and release (these data).

FIELD PROCEDURES

Thirty-seven plots (30 × 50 m) were established throughout the Reserve in a stratified (by forest type) random manner. Randomization was achieved by placing a 100 × 100 m grid over a base map showing forest types (Widoff 1985), and randomly selecting ordinate and abscissa grid lines, their intersection denoting a proposed plot's

southwest corner. Plot locations were rejected if they fell within 150 m of a previously selected location, the Reserve border, or a mapped boundary between forest types. Two locations were rejected in the field because they were disturbed by a recent event (presumably a known 1983 windstorm); these stands had approximately 50% canopy cover, meaning too few trees for this type of dendrochronological work. Rejected plot locations were substituted with additional random selections until the predetermined number of plots had been achieved for each forest type, that number being roughly proportional to the type's areal extent. Thus, twenty-one plots were established in the mixed woods type; five in the cedar seepage forest, four each in the red spruce forest and hardwood forests and three in the cedar swamps. Figure 1 shows plot locations.

On each plot we measured diameters and extracted increment cores (in 2000 and 2001) from all living trees ≥ 10 cm d.b.h. (1.37 m). Cores were extracted at breast height, and no attempt was made to estimate actual tree ages (i.e. years since germination) for the following reasons. First, even cores extracted at root-collar or lower-stem locations yield substantial underestimates of actual ages of shade-tolerant tree species (DesRochers & Gagnon 1997; Niklasson 2002). Second, seedlings of these species can become established and persist for many decades under shade. Thus, even if their actual ages could be determined, they may be poorly linked to disturbance events (Lorimer 1985; Veblen *et al.* 1990), the emphasis of this study. We thus refer to the number of annual rings at breast height as the recruitment age. We conducted a complete tally of saplings (stems < 10 cm d.b.h. but ≥ 2 m tall) in central 10 × 50 m transects in randomly chosen plots from each forest type (seven plots in mixed woods, three plots in the remaining types).

DENDROCHRONOLOGICAL PROCEDURES

Increment cores were dried, mounted and sanded to a fine polish using standard methods. For cores that missed the pith by less than

approximately 15 mm, a pith locator (Appelquist 1958) was used to estimate the number of rings to the pith. Incomplete cores (cores from trees with rotten centres or cores that did not pass near the pith) were excluded from age-class distributions but were evaluated for growth releases (see below). Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted using the marker-year method of Yamaguchi (1991), with statistical verification by COFECHA (Holmes 1983). Marker years included those with frost rings, light rings, false rings or unusual widths (Schweingruber 1996).

Evidence of past canopy disturbance derived from tree-ring data comes from two sources evident in surviving trees: abrupt and sustained increases in radial growth (growth releases) and rapid growth as the seedling achieved breast height (gap recruitments). Growth releases signify the sudden loss of an overtopping canopy and gap recruitment events suggest a tree experienced open, free-to-grow conditions during its transition from seedling to small tree. We note that gap recruitment does not imply germination in gaps. Seedlings of these shade-tolerant species may germinate under a closed canopy and exist for decades prior to their recruitment in gaps. Thus a gap-recruitment date, when present, provides a better estimate of gap formation than would germination date, even if it were determinable (see above). Each tree-ring series was evaluated for growth releases and gap-recruitment events, and both types of evidence were treated equally in the reconstruction of disturbance histories. For release detection, we used the method presented in Fraver & White (2005b), using comparisons of sequential 10-year running means (see Appendix S1 in Supporting Information for more detail). Gap recruited trees were deemed as such if the mean ring width for the first 5 years exceeded 1 mm (Lorimer 1980) and the subsequent growth pattern was declining, parabolic or flat (Frelich 2002).

DISTURBANCE CHRONOLOGIES AND METRICS

Growth releases and gap-recruitment events (henceforth releases) were tallied by decadal interval, allowing for the variable lag period between a disturbance and a tree's response, as well as the inherent difficulty in determining the actual date of disturbance (Lorimer & Frelich 1989). We converted the number of releases in each decade to estimates of canopy area disturbed following Lorimer & Frelich (1989), resulting in an area-based disturbance chronology for each plot (see Appendix S1). In forests dominated by shade-tolerant species, disturbance chronologies are more informative than age structures, because of the poor linkage between tree ages and disturbance events (as above; Lorimer 1985; Veblen *et al.* 1990). As disturbance chronologies extend further back in time, they become increasingly uncertain because more trees would have been lost through mortality. To partially mitigate this problem, we used only the period from 1870 forward in our analyses of temporal rates and patterns, and for the remaining analyses we truncated chronologies when sample size dropped below 10 trees per plot. By convention, we did not estimate disturbance rates for the most recent decade (1991–2000), because the release-detection method requires a full 10-year post-disturbance period for comparison. Further, the disturbance rate calculated for the latest decade evaluated (1981–1990) will necessarily underestimate the true rate because many gap-recruited trees will not have achieved the diameter necessary for coring.

Here, disturbance rate refers to the canopy area removed by disturbance per decade (as above) expressed as a percentage of the total canopy area from trees known to be present in that decade. Disturbance severity is used qualitatively, referring to the magnitude

of the disturbance rate thus defined; however, we define moderate-severity disturbances as having $\geq 30\%$ of the canopy removed within one decade. Rotation period refers to the time (in decades) it would take on average for all plots in the Reserve to experience a given disturbance rate (following Frelich & Lorimer 1991), calculated separately for specified rates (10%, 20%, 30%, 40% and 50%) (see Appendix S1).

INFLUENCE OF FOREST TYPE AND TREE COMPOSITION

We evaluated to what extent tree species composition influences disturbance characteristics using two complementary methods, namely repeated-measures analyses of variance (ANOVA) and the Mantel test for matrix correlation (Legendre & Legendre 2000). The former provides explicit tests of differences in disturbance rates and patterns between forest types, while the latter evaluates the extent to which disturbance rates vary across a gradient of species composition, ignoring forest-type designations.

For the repeated-measures ANOVA, disturbance rates in each decade (after arcsine transformation) served as the dependent variable. The ANOVA tested if disturbance rates varied across decades (within-subjects main effect), between forest types (between-subjects main effect), and the decade \times forest type interaction. The interaction specifically tests if temporal patterns (behaviour of the rates through time) vary by forest type (von Ende 1993). Preliminary data summaries suggested that the mean rate might be lower for the cedar swamps; this was tested by linear contrasts on the forest-type main effect. The number of decades used in the ANOVA was limited by those plots with shorter chronologies; hence, we include only the time period from 1870 onward. One mixed wood plot was eliminated from this analysis because it had adequate sample size only back to 1880. Thus, the ANOVA included 12 decades and 36 plots grouped into five forest types. Because the data violated the assumption of sphericity, the Huynh-Feldt adjustment to the univariate test of within-subjects effects was used (SAS Institute 1999).

The Mantel test required as input two symmetrical plot-by-plot matrices, one containing the distances between all pairs of plots based on relative basal area of tree species, the other containing distances based on disturbance chronologies. The Czekanowski index of dissimilarity was used as a measure of distance for both matrices (Greig-Smith 1983). Positive correlation between matrices would indicate that similarity between chronologies increases with increasing similarity in species composition. The Mantel test was based on arcsine-transformed chronologies (each consisting of 12 decades, as above) from 36 plots. Analyses were conducted in PCORD software (McCune & Mefford 1999).

Results

STAND COMPOSITION AND STRUCTURE

The Reserve is clearly dominated by shade-tolerant, late-successional tree species (Table 1). The six common species (*A. saccharum*, *F. grandifolia*, *B. alleghaniensis*, *P. rubens*, *A. balsamea* and *T. occidentalis*) represented 93% of all canopy trees sampled. Other shade-tolerant species, namely *Tsuga canadensis* (L.) Carr., *Acer pensylvanicum* L., *Ostrya virginiana* (Mill.) K. Koch, *Picea glauca* (Moench) Voss, and *P. mariana* (Mill.) B.S.P., together accounted for approximately 5% of all canopy trees. Species of intermediate tolerance, namely *P. strobus*, *A. rubrum* L., *B. cordifolia* Regel, *Fraxinus nigra*

Table 1. Relative basal area (as a percent) for tree species (above) and relative abundance (as a percent) for sapling species (below) by forest type. Species with relative basal areas or abundances < 2.0% in any forest type are not listed

	Hardwoods	Mixed woods	Spruce forest	Cedar seepage forest	Cedar swamp
Tree species relative basal area					
<i>Acer saccharum</i>	58.6	29.6	< 1	2.9	–
<i>Fagus grandifolia</i>	22.6	8.6	< 1	1.6	–
<i>Betula alleghaniensis</i>	5.8	10.1	1.0	9.6	1.0
<i>Picea rubens</i>	5.0	28.1	90.1	23.1	3.4
<i>Ostrya virginiana</i>	2.8	1.0	–	–	–
<i>Abies balsamea</i>	2.5	11.7	1.0	13.1	1.7
<i>Acer rubrum</i>	2.0	1.4	1.5	1.1	–
<i>Thuja occidentalis</i>	–	5.8	2.7	42.4	87.4
<i>Picea glauca</i>	–	2.1	–	3.2	4.3
<i>Pinus strobus</i>	–	< 1	2.4	< 1	1.5
Sapling species relative abundance					
<i>Acer saccharum</i>	20.8	14.1	–	8.5	< 1
<i>Fagus grandifolia</i>	52.0	35.2	2.8	3.1	–
<i>Betula alleghaniensis</i>	8.9	15.7	20.4	15.5	11.4
<i>Picea rubens</i>	9.4	7.2	32.5	20.7	18.3
<i>Ostrya virginiana</i>	4.6	2.6	–	1.0	–
<i>Abies balsamea</i>	< 1	6.9	22.1	26.2	27.0
<i>Acer rubrum</i>	–	< 1	3.0	1.0	< 1
<i>Thuja occidentalis</i>	–	–	–	2.1	26.2
<i>Acer pensylvanicum</i>	3.2	17.0	13.6	17.1	2.2
<i>Sorbus americana</i>	< 1	< 1	2.1	–	< 1
<i>Betula cordifolia</i>	–	< 1	3.1	–	–
<i>Fraxinus nigra</i>	–	–	–	4.7	13.6
Number of saplings per hectare	2563	3316	1628	2697	3735

Marsh., and *F. americana* L., together represented < 2% of all sampled trees. No shade-intolerant trees or saplings were found on any plots. Sapling composition and numbers (Table 1) attest to the importance of advance regeneration in this system, with composition generally reflecting that of the overstorey.

DISTURBANCE RATES

We found no evidence of stand-replacing disturbance during the period covered by this investigation (120–280 years, depending on plot): plot decadal disturbance rates rarely exceeded 30% canopy removal, with none exceeding 55%, and shade-tolerant tree species clearly dominated these stands. Reserve-wide peaks in disturbance activity occurred in the late-1700s–early-1800s, the 1870s and the 1920's. The overall mean decadal disturbance rate (all plots pooled) was 9.6% (median 6.5%). Rates averaged by forest type ranged from 5.1% to 11.9% (Fig. 2). The distribution of disturbance rates formed a strongly and positively skewed distribution, such that decades with higher rates were increasingly uncommon (Fig. 3). Rotation periods derived from this distribution point to quite long intervals between decades with moderate-severity disturbance: rates $\geq 30\%$ recur on a given plot roughly every 20 decades; rates $\geq 40\%$ every 41 decades and rates $\geq 50\%$ every 115 decades on average (Fig. 3).

Disturbance peaks revealed by our dendrochronological methods appear to have fostered tree recruitment throughout the Reserve. Recruitment ages, derived from complete increment cores, for five of the common species showed distinct

peaks that spanned two or more decades (Fig. 4; data pooled across plots), roughly following disturbance peaks. Interpretation of recruitment for the sixth common species, *T. occidentalis*, is quite limited because only 25% of the trees were available for age determination, owing to heart rot. Similarly, recruitment age structures for the five species intermediate in shade tolerance showed peaks generally following peaks in disturbance activity (Fig. 5).

INFLUENCE OF FOREST TYPE AND TREE COMPOSITION

ANOVA revealed that differences in disturbance rates between forest types were marginally significant ($F_{4,31} = 2.85$, $P = 0.04$), and linear contrasts on the between-subjects main effect indicated that cedar swamps had a mean decadal rate lower than that of the remaining forest types, whose rates did not differ. The decade-by-forest type interaction was not significant ($F_{44,341} = 1.38$, $P = 0.077$), suggesting little if any difference in the temporal patterns of disturbance between forest types. The marked temporal fluctuations in disturbance rates seen for all forest types (Fig. 2) were born out by the repeated-measures ANOVA, which showed variation across decades to be highly significant ($F_{11,341} = 6.60$, $P < 0.0001$). The Mantel test, which evaluates disturbance patterns across a gradient of tree species composition, indicated that composition and disturbance patterns were strongly correlated (Mantel test, $P = 0.008$, Mantel $r = 0.228$, approximated $t = 2.68$), such that the similarity between plot disturbance chronologies increased with increasing similarity in species composition.

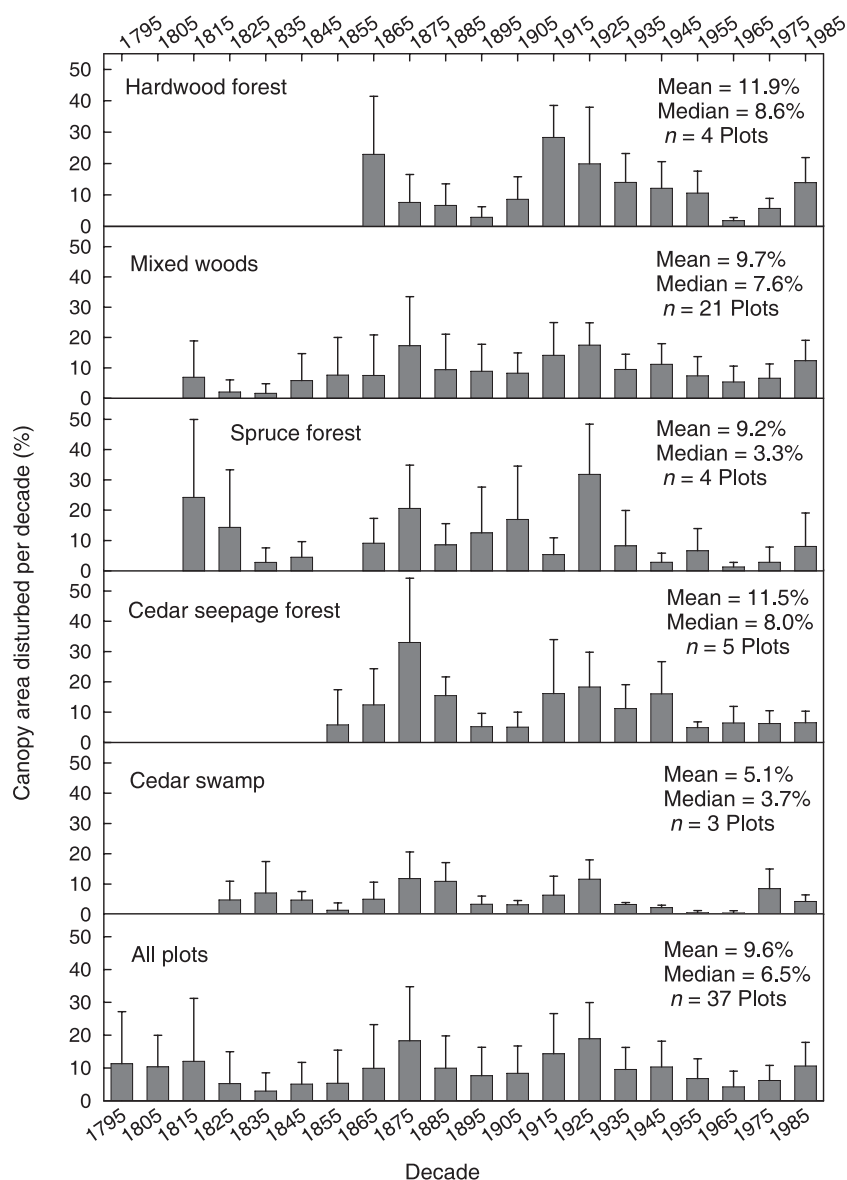


Fig. 2. Mean canopy area disturbed by decade for each of the five forest types. Mean values listed on the right result from averaging across all plots during the decades used in analyses (i.e. 1870 forward). Mean chronologies were truncated when the number of plots with adequate sample size dropped below three. Error bars represent standard deviations.

Discussion

DISTURBANCE HISTORY

The disturbance history that emerges from this work is one of repeated small-scale canopy disturbances, punctuated at times by pulses of moderate-severity disturbance caused by host-specific agents and windstorms (see Table S2). This pattern can clearly be seen in the positively skewed distribution of decadal disturbance rates (Fig. 3). Rotation periods derived from this distribution point to quite long intervals between decades with moderate-severity disturbance (Fig. 3). Rotation periods are similar to those determined, using methods similar to ours, for hemlock–hardwood forests of the Great Lakes region, despite differences in forest types and disturbance agents (Frelich & Lorimer 1991). The lack of host-specific agents of any consequence in hemlock–hardwood forests may

be counterbalanced by more frequent or severe wind storms in that region (Hanson & Lorimer 2007). Using six independent lines of evidence, Lorimer & White (2003) likewise estimated quite long intervals for major disturbance in the northeastern United States.

The mean decadal disturbance rates over the past 120 years are similar to those commonly reported for closed-canopy temperate forests (Seymour *et al.* 2002; Wolf *et al.* 2004). However, rates fluctuated markedly through time, as evidenced by the highly significant decade effect in the repeated-measures ANOVA. These fluctuations can also be seen on chronologies averaged by forest type, but to a lesser extent on the composite chronology for the entire Reserve (Fig. 2), as would be expected by including more plots and hence a larger sampling area (Frelich & Lorimer 1991). Plot-level fluctuations of similar magnitude have been reported from a variety of forest types (e.g. Veblen *et al.* 1994; Ziegler 2002). Thus, despite its

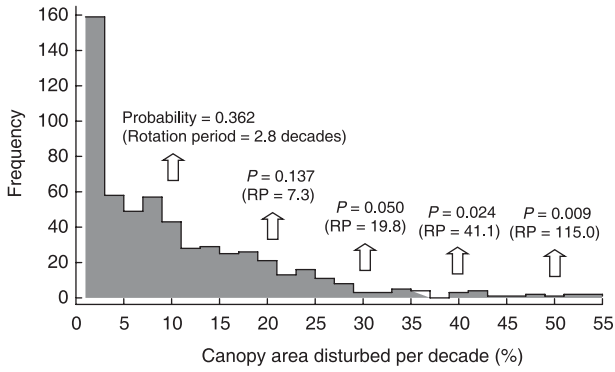


Fig. 3. Distribution of all disturbance rates (canopy area disturbed per decade), showing that higher rates are increasingly uncommon. Shown above selected disturbance rates are the probabilities of experiencing a decade with an equal or higher rate, as well as the corresponding rotation period (RP) in decades.

widespread use, the mean disturbance rate captures neither these temporal fluctuations nor the distribution of rates, both of which are needed to gauge historic variability in disturbance.

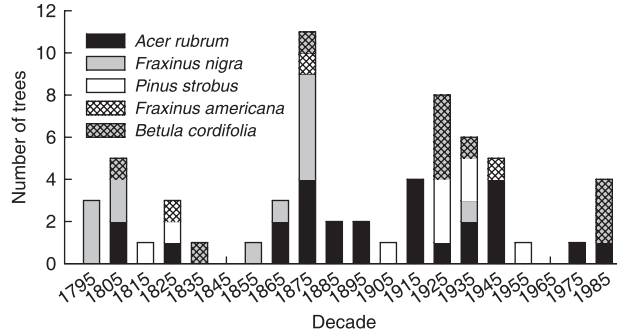


Fig. 5. Distributions of recruitment (i.e. breast height) ages for species intermediate in shade tolerance, showing that their recruitment generally follows peaks of moderate-severity disturbances occurring in the late-1700s–early-1800s, the 1870s and the 1920’s. These species are uncommon in the Reserve, representing < 2% of all canopy trees sampled.

The composite disturbance chronology, based on all plots (Fig. 2), shows peaks occurring in the late-1700s–early-1800s, the 1870s and the 1920’s. Peaks can readily be attributed to a number of documented agents (see Table S2). The highest

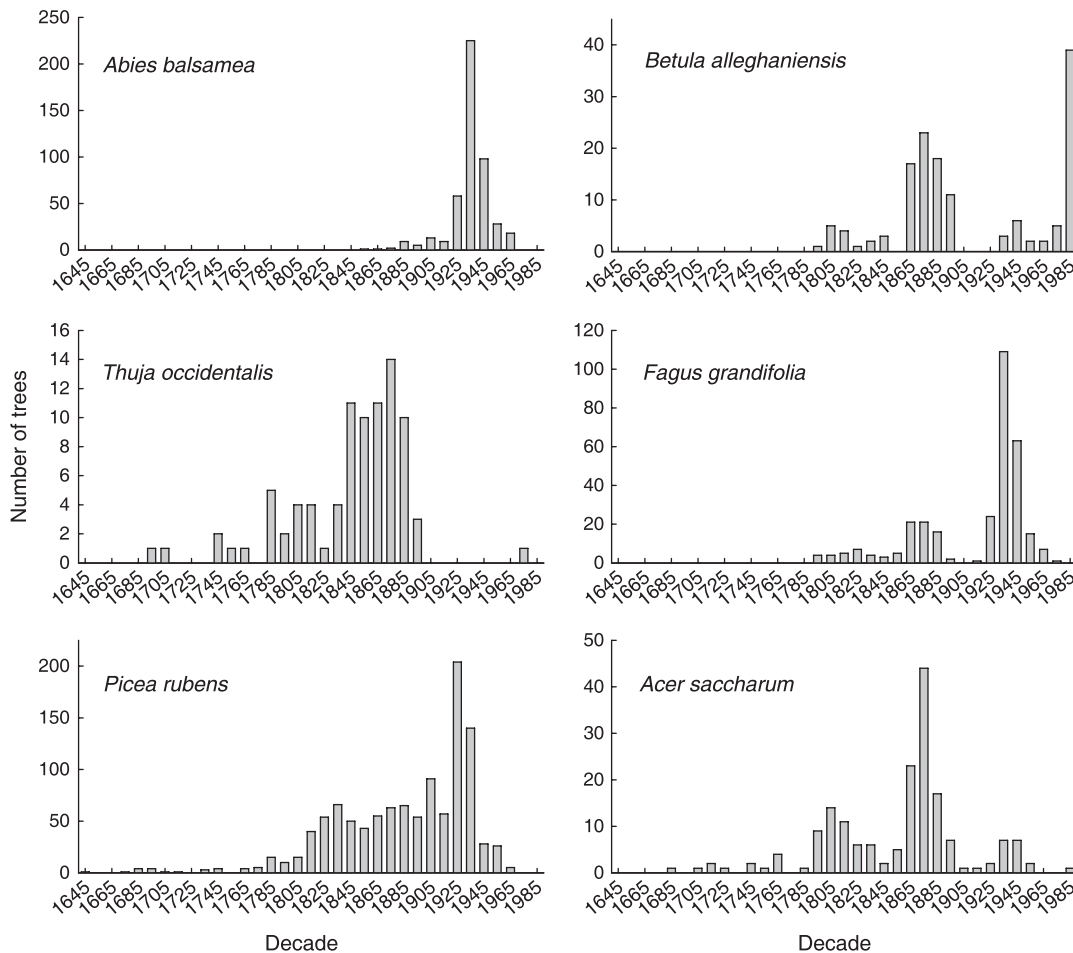


Fig. 4. Distributions of recruitment (i.e. breast height) ages for the six common species (all plots pooled). These species represent 93% of all canopy trees sampled. Data are derived from complete cores only; *T. occidentalis* is dramatically under-represented because of heart rot common to this species. Note that vertical axes are on different scales.

disturbance rates occurred during *C. fumiferana* (Clem.) (eastern spruce budworm) outbreaks (reaching 55% in the 1810s and 54% in the 1920s) and *D. rufipennis* Kirby (spruce bark beetle) outbreaks (reaching 53% in the 1870s). Similarly, Reserve-wide disturbance peaks coincide with hurricanes of 1788, 1815, 1869, 1874 and a major thunderstorm downburst of 1983. The coincidence of several insect outbreaks with windstorms confounds any assessment of their individual impacts.

Also of interest is the absence of fire. In addition to the results presented above, other lines of evidence rule out fire as a disturbance agent. First, northern Maine currently has the lowest lightning flash density of any location in the eastern United States (NOAA 2007). Second, members of our laboratory have encountered no fire-scarred trees in the Reserve during 6 years of extensive field work on this and related projects. Third, small-hollow sediment cores analysed from the Reserve show only minor peaks of charred material from several thousand years BP, with amounts generally declining thereafter (Schauffler 1998; Rowland 2006).

Disturbance pulses appear to be synchronized, albeit weakly, throughout the Reserve. Given that the common tree species and forest types are dispersed throughout the Reserve, synchronicity likely results from (i) host-specific insect populations that periodically reach outbreak levels and (ii) moderate-severity wind storms whose impact is felt throughout the Reserve.

A possible bias in our results is worthy of comment. During plot selection, two potential locations (one mixed-wood, one cedar seepage forest) were rejected in the field because a recent disturbance had removed approximately 50% of the canopy (see Field Procedures). Had these locations experienced repeated severe disturbances, their exclusion would result in an underestimate of Reserve-wide disturbance rates. However, because they were still dominated by shade-tolerant species and were not in unusual or exposed landscape settings, we assume this bias to be minimal.

INFLUENCE OF FOREST TYPE AND TREE COMPOSITION

To the best of our knowledge, no previous work has explicitly addressed differences in rates or temporal patterns of disturbance between forest types within an old-growth landscape. Contrary to our first hypothesis, ANOVA results indicated that the red spruce forest type did not have the highest disturbance rate, despite the fact that the 120-year period analysed included one spruce bark beetle outbreak and two budworm outbreaks. Our results suggest that northern-white cedar swamps had a mean disturbance rate lower than the other four forest types, whereas no other types differed. The low disturbance rate found in this forest type may be attributable to a methodological limitation. Trees in northern-white cedar swamps occur in clumps, resulting in quite patchy canopy cover even in the absence of disturbance. The advance regeneration and smaller trees in the interstices may not be limited primarily by light and would therefore be less responsive, in terms of radial growth, to the loss of a canopy tree. Given that

the dendrochronological methods employed here are meant to detect overhead canopy disturbances, they may not perform well when applied to such irregularly structured canopies (Frelich 2002; Fraver *et al.* 2008). Further, the temporal patterns of disturbance (i.e. behaviour of the rates through time) did not differ among forest types. The absence of clear differences between forest types could be explained in part by the large degree of species overlap between types. For example, *P. rubens* forms a significant component of three forest types; *A. saccharum* and *T. occidentalis* are the leading dominants in two types; and *F. grandifolia*, *A. balsamea*, and *B. alleghaniensis* form a significant component of two types (Table 1).

However, if we ignore forest-type classifications and focus instead on gradients of tree species composition, we see that the similarity between plot disturbance chronologies increased with increasing similarity in species composition (assessed by the Mantel test). That is, the relative abundance of component tree species clearly influences the disturbance rates and temporal patterns registered in a forest stand. This correlation likely results from the prevalence of host-specific disturbance agents, as well as species' relative susceptibilities to windthrow. Spruce budworm outbreaks provide a striking example: plots with relatively abundant *P. rubens* or *A. balsamea* – regardless of their forest type – show pulses in disturbance activity coincident with known budworm outbreaks. Similarly, plots with abundant *P. rubens* show pulses coincident with documented hurricanes, given this species' susceptibility to windthrow (Canham *et al.* 2001). Thus, categorizing stands into forest types for the purpose of describing disturbance regimes, though essential for many theoretical and applied endeavours, may obscure differences owing to the relative abundances and susceptibilities of component species.

DISTURBANCE AND MAINTENANCE OF LATE-SUCCESSIONAL SPECIES

The prevalence of low-severity disturbances (Fig. 3) indicates the disturbance regime has been dominated by single or multiple treefalls over the 120–280 years (depending on plot) covered by this investigation. The fact that plot decadal disturbance rates rarely exceeded 30% canopy removal, with none exceeding 55%, lends support for our second hypothesis, namely that disturbances were not stand replacing. However, periodic moderate severity disturbances ($\geq 30\%$ canopy removal per decade) occurred on plots of each forest type except the northern-white cedar swamp. This amount of canopy removal suggests gap sizes large enough to admit mid-tolerant or intolerant species, especially if accompanied by soil disturbance. Yet shade-tolerant, late-successional species have maintained dominance in all forest types and throughout the landscape.

Periods of quiescence between disturbance pulses, typically spanning several decades, allow the accrual of shade-tolerant advance regeneration sufficient in number to ensure that these species proceed to the canopy following even moderate-severity disturbance. We note that all six common tree species were abundant as advance regeneration (Table 1) and that

individuals of this stature are seldom damaged by any of the disturbance agents identified here. The importance of advance regeneration has long been recognized for several of these forest types (Westveld 1931; Leak *et al.* 1987), and the persistence of shade-tolerant species under moderate severity disturbance has been shown in stand-level studies (Batzer & Popp 1985; Webb & Scanga 2001; Fraver & White 2005a; Hanson & Lorimer 2007). However, this has rarely been demonstrated at the landscape level (but see Frelich & Lorimer 1991; Bouchard *et al.* 2007), nor for a variety of forest types within a landscape.

Nevertheless, peaks in disturbance were presumably sufficient to admit species intermediate in tolerance, such as *P. strobus*, *A. rubrum*, *B. cordifolia*, *F. nigra*, and *F. americana*. Together these species represent < 2% of all plot trees within the Reserve. Their combined age-class distribution (Fig. 5) reveals peaks in recruitment generally following Reserve-wide disturbance peaks. Their recruitment, however, does not represent a directional shift in species composition, rather a minor enrichment at best. Even more surprising may be the rarity of shade-intolerant tree species, such as *B. papyrifera* Marsh. and *Populus* species, given their abundance in the surrounding harvested landscape (suggesting a local seed source) and throughout the region. Neither of these taxa was found on our study plots, and extensive reconnaissance throughout the Reserve revealed few *B. papyrifera* trees and no *Populus* species. These species were likewise poorly represented in the pre-settlement forests of this region (Dana 1930; Lorimer 1977).

The persistence of shade-tolerant species results in a mosaic of patches in various stages of structural development, not various stages of compositional succession.

Although large-scale, severe disturbance might temporarily shift composition toward early-successional species, the fact that we detected no such events precludes calculation of their probability or rotation period, which may in fact be longer than several dominant species have existed in any abundance in this region. *P. rubens*, currently the most abundant tree species in the Reserve, rose to significance only 1000–2000 years BP following a region-wide climate shift to cooler, moister conditions; *A. balsamea* also increased in abundance during this time, although less dramatically so (Schauffler & Jacobson 2002).

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Detailed dendrochronological methods.

Table S1 Known disturbances in northern Maine.

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