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Stand dynamics and structure of old-growth *Fraxinus nigra* stands in northern Minnesota, USA

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Abstract

Black ash (*Fraxinus nigra* Marsh.) forests of north-central North America are currently threatened by the non-native emerald ash borer (*Agrilus planipennis*, EAB). Despite the wide distribution of *F. nigra* ecosystems, and the concern over EAB impact, little is known about their structure and natural stand dynamics. We sampled six old-growth *F. nigra* stands to assess structure, composition, tree recruitment, and past disturbance. Dendrochronological results revealed that disturbance rates fluctuated markedly over the past 200 years or more, but remained relatively low, suggesting small- to moderate-scale disturbances. Recruitment age structures revealed that (*i*) *F. nigra* is able to maintain long-term dominance through extended longevity as a canopy tree, and (*ii*) these systems have fairly continuous recruitment over time, with most sites showing *F. nigra* recruitment in every decade in the chronology. We speculate that recruitment is coupled with water table fluctuations, in addition to canopy disturbance, as these stands are subject to both frequent flooding and effective soil drought (given the shallow root systems). The low rates of past canopy disturbance and associated gap-phase replacement by *F. nigra* highlight the potential for dramatic shifts in these systems following emerald ash borer invasion and subsequent canopy tree mortality.

Key words: black ash, dendroecology, emerald ash borer, gap dynamics, stand dynamics, moderate-severity disturbance

Résumé

Les forêts de frênes noirs (*Fraxinus nigra* Marsh.) du centre-nord de l'Amérique du Nord sont actuellement menacées par l'agrile du frêne (*Agrilus planipennis*, EAB), une espèce non indigène. Malgré la large distribution des écosystèmes de *F. nigra* et l'inquiétude concernant l'impact de l'agrile du frêne, on sait peu de choses sur leur structure et la dynamique naturelle des peuplements. Nous avons échantillonné six peuplements anciens de *F. nigra* pour évaluer la structure, la composition, le recrutement des arbres et les perturbations passées. Les résultats dendrochronologiques ont révélé que les taux de perturbation ont fluctué de façon marquée au cours des 200 dernières années ou plus, mais sont restés relativement faibles, ce qui suggère des perturbations à petite ou moyenne échelle. Les structures d'âge du recrutement ont révélé que (*i*) *F. nigra* est capable de maintenir une dominance à long terme grâce à une longévité prolongée en tant qu'arbre de la canopée, et (*ii*) ces systèmes ont un recrutement assez continu dans le temps, la plupart des sites montrant un recrutement de *F. nigra* dans chaque décennie de la chronologie. Nous supposons que le recrutement est couplé aux fluctuations de la nappe phréatique, en plus de la perturbation de la canopée, car ces peuplements sont soumis à la fois à des inondations fréquentes et à une sécheresse effective du sol (étant donné la faible profondeur des systèmes racinaires). Les faibles taux de perturbation de la canopée dans le passé et le remplacement par *F. nigra* qui y est associé soulignent le potentiel de changements dramatiques dans ces systèmes après l'invasion de l'agrile du frêne et la mortalité subséquente des arbres de la canopée. [Traduit par la Rédaction]

Mots-clés : frêne noir, dendroécologie, agrile du frêne, dynamique des espaces, dynamique des peuplements, perturbation de gravité modérée

1. Introduction

Forest ecosystems can be dramatically altered when non-native insects eliminate a foundational tree species, thereby causing shifts in food webs, energy flux, hydrology, and biodiversity (Ellison et al. 2005). Increased globalization, resulting in greater transcontinental trade, may exacerbate the spread of non-native organisms (Roy et al. 2014). In addition, a changing climate may further enhance their spread and thus intensify the ultimate impact of such organisms (Ayres and Lombardero 2000; Logan et al. 2003). These concerns are most pronounced in situations where the non-native insect is host-specific, and the tree host represents a dominant tree species (Lovett et al. 2006).

One such example is the emerald ash borer (*Agrilus planipennis* Fairmaire, EAB), a non-native, invasive insect from Asia that has been killing native ash (*Fraxinus* species) trees in eastern North America (Herms and McCullough 2014). The EAB has been actively spreading throughout central and eastern North America since its detection in 2002. It is causing widespread mortality to three of the region's native ash species (Cappaert et al. 2005; Kashian and Witter 2011). Two of these species, white ash (*Fraxinus americana* L.) and green ash (*Fraxinus pennsylvanica* Marsh.), often occur in admixtures with other hardwoods and seldom form pure stands (Aaseng et al. 2003). In contrast, a third species, black ash (*Fraxinus nigra* Marsh.), often forms pure or nearly pure stands in poorly drained landscape positions (Palik et al. 2021*a*) and serves as a foundational species in these settings (Youngquist et al. 2017). As such, EAB is a particular threat to *F. nigra* forests because mortality of this species would result in the loss of a major forest type and associated functions (Palik et al. 2021*a*). Further, the demise of *F. nigra* from EAB will no doubt be exacerbated by climate change, which is projected to favor the northward expansion of EAB in the Great Lakes region of North America (Liang and Fei 2014). With the loss of overstory *F. nigra*, and the concomitant rise of the water table due to reduced transpiration (Diamond et al. 2018), these forests may convert to open marshes dominated by speckled alder (*Alnus incana* (L.) Moench) and graminoids (Erdmann et al. 1987; Palik et al. 2012). This conversion would have profound implications for site productivity, local hydrology, habitat quality, and timber resources (Youngquist et al. 2017), as well as cultural and spiritual traditions of Native Americans and First Nations (Costanza et al. 2017).

Despite the widespread occurrence of *F. nigra* ecosystems, particularly in the Great Lake States region of North America, little is known about their stand structure, recruitment, natural disturbance, and successional patterns (but see Tardif and Bergeron 1999; Springer and Dech 2021). The lack of this basic information hinders our ability to prescribe transitionary silvicultural treatments following the potential demise of this forest type or restoration treatments that emulate natural disturbance (Palik et al. 2020), something that may be particularly important if a solution to the EAB can be found. Thus, one motivation for our work was to characterize the structure, recruitment, and history of natural disturbance of *F. nigra* wetland forests before the species and ecosystem is lost or greatly altered by EAB and climate change. This information could readily be acquired from a detailed study, including dendrochronological applications, of extant old-growth *F. nigra* forests conducted before the loss of this forest type. The absence of similar pre-mortality studies accounts for our poor understanding of the chestnut–oak (*Castanea*–*Quercus*) forests of the eastern US prior to chestnut blight (Keever 1953) and the mixed hardwood forests of northern New England before beech-bark disease (Houston 1975).

With this need in mind, the objectives of this study were to (*i*) quantify the variability in stand structure and composition in old-growth *F. nigra* forests, and (*ii*) characterize the tree recruitment patterns and historical disturbances of these forests. To pursue these objectives, we combined detailed forest inventories, with extensive dendrochronological analyses for six old-growth *F. nigra* sites in northern Minnesota, USA, that have not yet been affected by EAB. Findings from this study will benefit recent concerted efforts to identify appropriate management strategies for this forest type, given the introduction of EAB and expected impacts of climate change (D'Amato et al. 2018).

2. Methods

2.1. Study area and sites

We located six old-growth *F. nigra* study sites in northern Minnesota, USA, which we defined as (*i*) being in late developmental stages and (*ii*) having no historical or visible evidence of past harvesting. We chose old-growth sites in hopes of obtaining long tree-ring records, allowing us to extend the disturbance histories relatively far back in time. Potential sites were identified through consultation with US Forest Service staff, as well as state and county agencies. All sites lie within the Laurentian Mixed Forest Province (Aaseng et al. 2003). The climate in this region is cold-temperate continental, with short cool summers and long severe winters. Mean monthly temperatures range from −13.7 °C in January to 16.5 °C in July, and mean annual precipitation is 74.2 $\text{cm}\cdot\text{year}^{-1}$ (PRISM Climate Group 2015, data 1981–2014). Soil texture varied among sites; however, all sites have a confining clay layer that impedes drainage. Poor drainage, coupled with little or no relief, results in ponding early in the growing season, typically persisting through mid-July (Benedict and Frelich 2008; Slesak et al. 2014).

The Minnesota native plant community classification system (Minnesota Department of Natural Resources 2003) classifies these sites as either northern wet ash swamps or northern very wet ash swamps. These are the only two *F. nigra* forest communities recognized for northern Minnesota, and the distinction between them is subtle, determined primarily by duration of flooding and herbaceous understory composition. Importantly, these community types occupy poorly drained basins, unassociated with streams, rivers, ponds, lakes, or fens. Thus, the flooding they experience results from a rising water table, not from beaver activity or overland flow from water bodies.

2.2. Field sampling

We established one 70.7 m × 70.7 m (0.5 ha) plot at each of the six sites in 2011. Plots were aligned true north–south and east–west. Sampled stands were similar in size, ranging from 25 to 32 ha; all stands featured scattered canopy gaps resulting primarily from windthrow. To reduce subjectivity in plot placement, we placed plots in the geographical centers of each stand. Within each plot, we recorded species, diameter at breast height (dbh, 1.37 m), and crown position (four-class system as per Smith et al. 1997) for all living and standing dead trees (stems ≥10 cm dbh). For all living trees, we extracted one increment core at breast height using a standard 5.2 mm increment borer to determine growth patterns and estimate recruitment ages. However, for one site (Stony Point, a designated Research Natural Area), the research permit stipulated that we core every other tree. The protected status of several sites prevented collecting radial cross-sections from dead stems, which could bolster dendrochronological analyses. Instead, we extracted large-diameter (12 mm) increment cores from dead stems, both standing and fallen, when not precluded by decay. Use of the large borer increases the chance of obtaining useable samples from partially decayed wood (Fraver et al. 2017). In most cases, cores from dead trees had rotten sapwood, but growth patterns and recruitment dates could be obtained from intact heartwood once cross-dated. In total, 1834 cores were used in this study (from both live and dead trees), 81% of which were *F. nigra*. Finally, we tallied all saplings by species (individuals >1.37 m in height, less than 10 cm dbh) in four randomly chosen transects (5 m × 70.7 m) at each stand. We recognize that saplings may have arisen from seed or by vegetative reproduction (Erdmann et al. 1987; Tardif et al. 1994); however, we did not attempt to make that distinction while sampling.

At each site, we inventoried downed coarse woody material (CWM) to shed light on past disturbances and to augment the structural description for these stands. The inventory was conducted using the line-intercept method (van Wagner 1968), based on eight transects (four 50 m at ordinal directions and four 35 m at cardinal directions) radiating spoke-like from plot center, for a total of 340 m of transect length per plot, which produces an acceptable level of precision (Fraver et al. 2018). For each CWM piece with a diameter of ≥10 cm at the transect intersection, we recorded diameter at intersection, species, and decay class (five-class system as per Sollins 1982). The volumes of decay classes 4 and 5 pieces were reduced accordingly to account for gradual collapse through decay (Fraver et al. 2013; Campbell et al. 2019).

2.3. Laboratory procedures and analyses

Increment cores were affixed to wooden mounts and sanded to a fine polish. Ring widths were measured to the nearest 0.01 mm using a Velmex (Bloomfield, NY, USA) sliding-stage stereomicroscope. Cross-dating of both living and dead material was conducted using the marker-year method of Yamaguchi (1991), with statistical verification by COFECHA (Grissino-Mayer 2001). To refine ring counts for cores that missed the pith, we applied Applequist's (1958) pith location method.

Because *F. nigra* seedlings can become established and persist for long periods under shade (up to 60 years; Springer and Dech 2021), we consider an individual to be recruited into the stand only when it achieves breast height (i.e., coring height). Thus we did not attempt to estimate tree ages since germination or sprouting; instead, we used the number of annual rings at breast height as the recruitment age. Recruitment ages from cross-dated deadwood were included in recruitment age-class distributions.

Evidence of past disturbance can be detected in tree-ring series as rapid growth at the time the tree reached breast height (i.e., *gap-recruitment* events) and abrupt increases in radial growth (i.e., *growth releases*), as both responses suggest the loss of overtopping canopy trees (Lorimer 1985; Lorimer and Frelich 1989). For forests that include shade-tolerant tree species, where small individuals can persist for decades under shade, the use of gap-recruitment events and growth releases provides an improvement over tree ages (since germination) for detecting past canopy disturbances (Lorimer 1985). Thus each tree-ring series was evaluated for gap-recruitment events and growth releases.

Trees were considered to be gap-recruited if the mean ring width for the first 5 years in the series exceeded 1.2 mm (Frelich 2002; D'Amato and Orwig 2008), and the subsequent growth pattern was declining, parabolic, or flat (Frelich 2002). Growth releases were detected using the absolute-increase method (Fraver and White 2005), with an absolute-increase threshold set at 0.62 mm for *F. nigra*, determined using methods presented in Fraver and White (2005). These methods are meant to detect the disturbance-caused loss of overtopping canopy trees and are thus equivalent to the "major" releases common in the literature. We used a 10-year window for release detection (growth 10 years following the event compared to growth 10 years prior), which is intended to exclude short-term growth anomalies due to climatic factors (Lorimer and Frelich 1989). Using the tallied growth releases and gap-recruitment events (henceforth "releases"), we constructed a disturbance chronology for each site by converting the number of releases observed in each decade to estimates of percent canopy area disturbed within the plot, following methods developed by Lorimer and Frelich (1989). We extended each site's disturbance chronology back in time to the point where the number of living trees dropped below 20.

3. Results

3.1. Stand structure and composition

Fraxinus nigra dominated structure and composition at all six sites, with a mean relative basal area of 81% (range 68%–93%) across sites (Table 1). Pooled data from the six sites showed a mean living-tree basal area of 30.6 $m^2 \cdot ha^{-1}$ (range 24–38), density of 659 trees·ha^{-1} (range 444–902), and density of large (>40 cm dbh) living trees of 48 trees·ha^{-1} (range 12–104) (Table 2). Mean CWM volume was 126 $m^3 \cdot ha^{-1}$, although this also varied markedly among sites (range 70–243). *Fraxinus nigra* dominated the CWM pool, accounting for 59% of total volume (excluding pieces that could not be identified to species), with American elm (*Ulmus americana* L.) and northern white-cedar (*Thuja occidentalis* L.) each representing 13% (sites pooled). Mean sapling density (all species combined) was 593 stems·ha^{-1}, although density varied among sites and was patchy within a site. *Fraxinus nigra* was the most abundant sapling species at all sites, representing on average 63% of all saplings tallied. Table 2 lists structural attributes for each site.

Several diameter distribution patterns were observed across sites (Fig. 1), ranging from unimodal (Stony Point) and

Table 1. Overstory composition of the six old-growth *Fraxinus nigra* study sites.

Species	Kupcho Run	Lake Williams	Round Lake	Stony Point	Toimi Creek	Waskish Trail
Fraxinus nigra	68.2	859	93.2	77.3	77.0	81.4
Abies balsamea	7.3	<1	1.6	—	2.4	12.6
Thuja occidentalis	—	6.6	—	—	17.3	—
Fraxinus pennsylvanica	2.4	—	1.8	18.4	—	—
Tilia americana	11.2	—	<1	2.5	—	—
Betula alleghaniensis	—	5.9	—	<1	2.8	—
Ulmus americana	1.6	<1	2.6	<1	—	1.1
Picea glauca	3.3	—	—	—	<1	1.8
Populus tremuloides	3.7	—	—	—	—	—
Betula papyrifera	—	<1	—	—	<1	2.7
Quercus macrocarpa	2.3	—	<1	<1	—	<1
Acer rubrum	—	1.4	—	—	—	—

Note: Values are relative basal area (%) of live trees with diameters of ≥10 cm at breast height.

Table 2. Structural characteristics of the six old-growth *Fraxinus nigra* study sites, including trees (dbh ≥ 10 cm), saplings (individuals >1.37 m in height, less than 10 cm dbh), and downed CWM.

	Live trees		Large trees	Snags		CWM	Saplings (stems·ha^{-1})	
Site	BA·ha^{-1}	Stems·ha^{-1}	Stems·ha^{-1}	BA·ha^{-1}	Stems·ha^{-1}	Vol.·ha^{-1}	Total	*F. nigra*
Kupcho Run	27.9	666	44	2.4	32	243	510	462
Round Lake	34.0	524	80	1.7	104	70	328	288
Stony Point	38.0	444	104	0.6	6	84	784	394
Lake Williams	30.0	902	28	1.6	32	122	454	284
Toimi Creek	29.8	782	12	1.8	36	120	420	248
Waskish Trail	24.0	638	18	2.7	90	120	1062	572
Mean	30.6	659	48	1.8	50	126	593	375
(Std. Dev.)	(4.9)	(167)	(37)	(0.7)	(38)	(61)	(277)	(125)

Note: Live tree basal area (BA) is in m^2, coarse woody material (CWM) volume in m^3, large trees are those >40 cm dbh.

variable (Lake Williams, Toimi Creek, Waskish Trail) to increasing Q (Round Lake) and rotated sigmoid distributions (Kupcho Run; based on classification in Janowiak et al. 2008). *Fraxinus nigra* was generally the dominant species across size classes, with other species more abundant in smaller diameter classes.

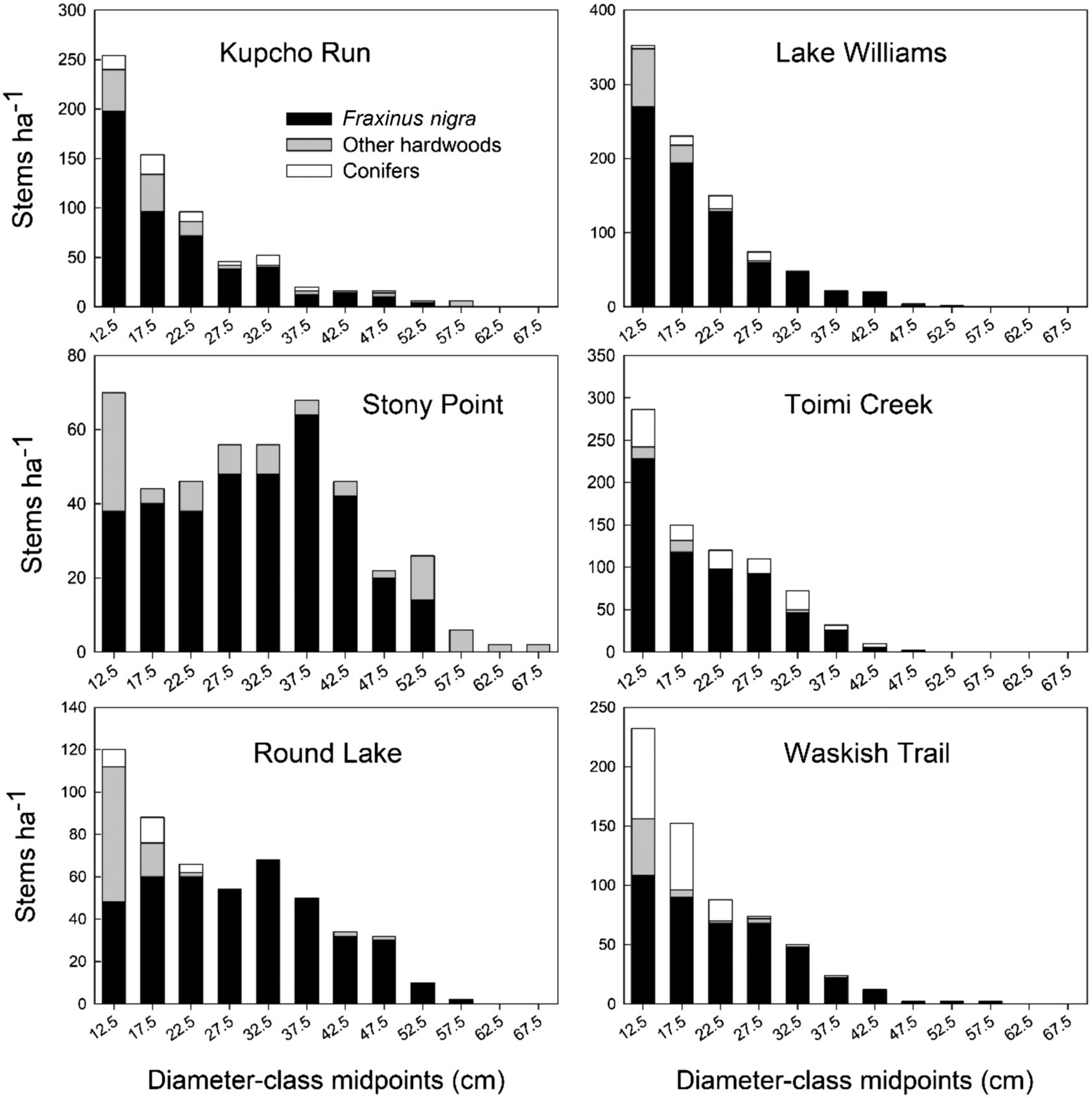
3.2. Historical disturbance and recruitment

The disturbance chronologies varied markedly among sites in terms of the severity (canopy area disturbed) and timing of past disturbance (Fig. 2). Mean %canopy area disturbed per decade ranged from 1.4% to 9.2% among sites, with an overall mean of 4.7% (median = 1.6%). The chronologies revealed no evidence of stand-replacing disturbance during the reconstructed period; however, the Kupcho Run site experienced 65% canopy loss in the 1980s, and Stony Point experienced ca. 30% canopy loss in both the 1920s and 1930s. No disturbance peaks were common to all sites (Fig. 2).

Based on sound *F. nigra* cores (live and dead trees, sites pooled), 12% were recruited in gaps (i.e., rapid early growth indicating recruitment under an open canopy). Of the live trees currently in the canopy, 35% showed one growth release before reaching the canopy, 4% showed two releases, and <1% showed three releases. A large percentage — 61% — showed no release; these exhibited a variety of growth patterns, ranging from persistent slow growth to fluctuating growth, but with fluctuations insufficient to meet our release criteria.

Our results emphasize the longevity of *F. nigra* relative to most co-occurring species: numerous *F. nigra* trees had recruitment ages (i.e., number of years since achieving breast height) exceeding 200 years, and several exceeding 300 years (Fig. 3). Maximum recruitment ages for several of the long-lived individuals include bur oak (*Quercus macrocarpa* Michx.) (320 years), *F. nigra* (315 years), *T. occidentalis* (269 years), white spruce (*Picea glauca* (Moench) Voss) (237 years), and *U. americana* (161 years). Recruitment age-class distributions show clear evidence of continuous *F. nigra* recruitment, with trees being recruited in nearly every decade of the reconstructed period (Fig. 3). Recent decades show an apparent decline in *F. nigra* recruitment and minor recruitment of non-ash species, including *T. occidentalis*, basswood (*Tilia americana* L.), balsam fir (*Abies balsamea* (L.) Mill.), yellow birch (*Betula alleghaniensis* Britton), aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), *P. glauca*, *Q. macrocarpa*, and red maple (*Acer rubrum* L.). Peaks in recruitment only weakly coincided with peaks in disturbance, based on a visual comparison of Figs. 2 and 3.

Fig. 1. Diameter distributions for six old-growth *Fraxinus nigra* wetland forests in northern Minnesota, USA. Note that vertical axes are on different scales.

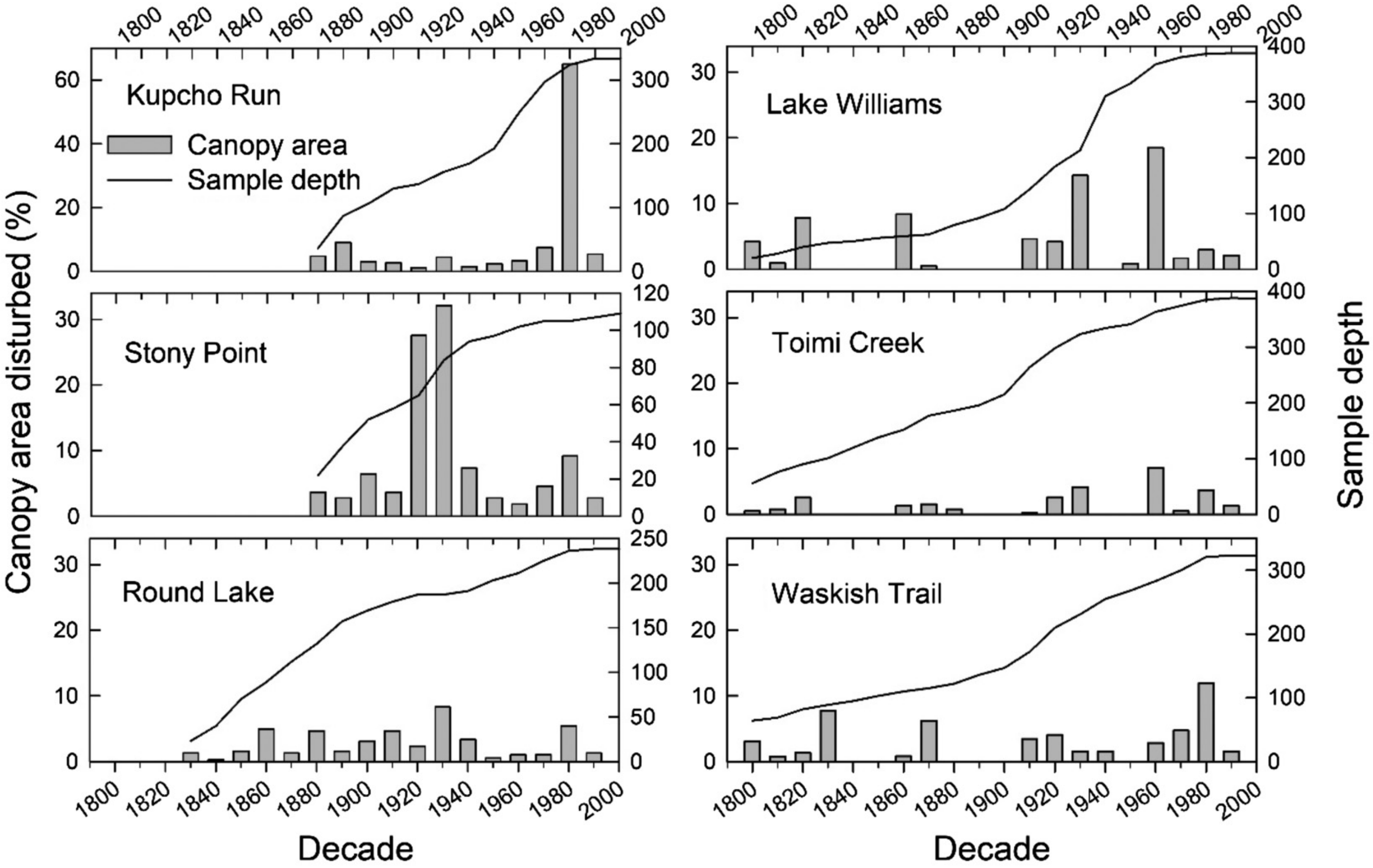


4. Discussion

4.1. Stand structure and composition

The tree species composition found on our sites corresponds well with descriptions of mature lowland *F. nigra* stands in the US Lake States (Kurmis and Kim 1989; Palik et al. 2021*a*), recognizing that the former abundance of *U. americana* in the overstory (reported in Kurmis and Kim 1989) has been reduced due to Dutch elm disease (fungus of the genus *Ophiostoma*), which caused widespread mortality of *U. americana* in the 1970s and 1980s (French 1993). *Fraxinus nigra* clearly dominated our stands (representing 81% of the basal area overall), with lesser amounts of *A. balsamea*, *T. occidentalis*, and *F. pennsylvanica* (each at 4%). Basal areas in these

Fig. 2. Disturbance chronologies for six old-growth *Fraxinus nigra* wetland forests in northern Minnesota, USA. Bars represent reconstructed percentage of canopy area disturbed per decade, and sample depth refers to the number of canopy trees contributing to the chronology. Note that the vertical axes are on different scales.



stands (mean 30.6 $m^2 \cdot ha^{-1}$) are also within the ranges reported for mature *F. nigra* stands in the region (Kurmis and Kim 1989; Townshend 2012). Although descriptions of old-growth *F. nigra* deadwood structures are unavailable for comparison, our snag and CWM volumes are similar to those reported for other old-growth hardwood forests in the region (Goodburn and Lorimer 1998). Nevertheless, both snag abundance and CWM volumes varied widely among our sites, as a result of varying disturbance histories in recent decades.

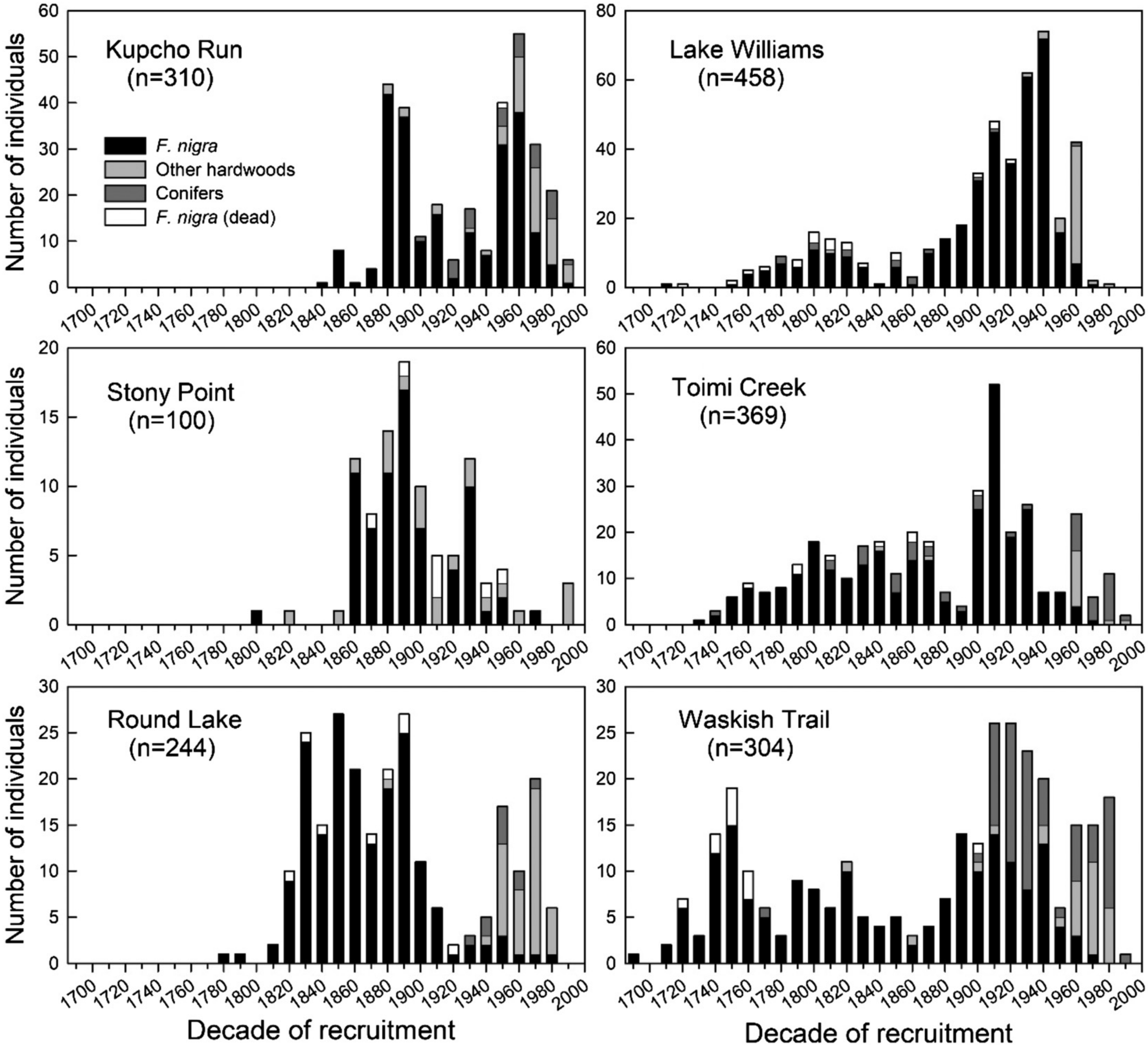
Live-tree diameter distributions largely displayed descending monotonic forms, which is consistent with distribution shapes documented for mature and old-growth *F. nigra* stands elsewhere in the Great Lakes region (Erdmann et al. 1987; Tardif and Bergeron 1999). Despite the functional classification of *F. nigra* as intermediate in shade tolerance, its high representation across all size classes is more consistent with population structures documented for old-growth systems dominated by shade-tolerant canopy species (Westphal et al. 2006; D'Amato et al. 2008). The limited representation of other species across size classes, particularly larger diameters, underscores the potential for significant shifts in live-tree structural conditions and associated functions (e.g., aboveground carbon storage) with EAB arrival to these areas.

4.2. Historical disturbance and recruitment

Numerous *F. nigra* trees had recruitment ages exceeding 200 years, and several exceeded 300 years. Tardif and Bergeron (1999) found very similar ages, and Kurmis and Kim (1989) report several *F. nigra* trees over 200 years of age. Importantly, all sites showed strong evidence of continuous *F. nigra* recruitment, with recruitment occurring at each site in nearly every decade under study. Springer and Dech (2021) also report multi-cohort *F. nigra* age structures from Ontario. Our age structures indicate that recruitment of species other than *F. nigra* was largely restricted to the latest century, although most of these species (*T. occidentalis*, *F. pennsylvanica*, and *T. americana*) are also long-lived. The recruitment of these species in recent decades might portend a shift in species composition; however, we found that a majority of saplings at each site were *F. nigra*.

Our disturbance chronologies depict a history of sporadic low- to moderate-severity canopy disturbances across the six sites, with the overall disturbance rate being quite low (mean

Fig. 3. Number of trees recruited (i.e., achieving breast height) per decade for six old-growth *Fraxinus nigra* wetland forests in northern Minnesota, USA, showing nearly continuous recruitment of *F. nigra* over time (n = number of tree-ring series analyzed). Note vertical axes are on different scales.



of 4.7% canopy area disturbed per decade). The chronologies revealed no evidence of stand-replacing disturbance during the reconstructed period. Disturbance rates in three of the six sites did not exceed 10% in any decade during the reconstructed period. By far, the greatest decadal disturbance rate (65% of the canopy disturbed) occurred at Kupcho Run during the 1980s. In addition, the Stony Point site experienced ca. 30% canopy area disturbed in the 1920 and 1930s.

The 1980s disturbance peak seen at Kupcho Run presumably resulted from the introduced Dutch elm disease prevalent at that time. The volume of *U. americana* CWM at this site ($43\ m^3 \cdot ha^{-1}$) was considerably higher than that at any other site, suggesting abundance of this species prior to arrival of the disease. The minor disturbance peaks at this same time at Stony Point, Round Lake, and Waskish Trail are also likely attributed to Dutch elm disease, as *U. americana* was present as CWM and (or) snags at those sites as well.

Tardif and Bergeron (1999) found similarly low disturbance rates in *F. nigra* stands of Quebec, and found, as we did in the current study, that evidence of canopy disturbance was not synchronized among study sites within their study landscape. These generally low disturbance rates, coupled with the lack of synchronized disturbance peaks, point to an absence of large-scale, region-wide disturbance agents. The absence of such disturbances in our study may be attributed to the low landscape positions occupied by these sites, which protect them from wind, and the wet site conditions, which protect them from fire.

Our results suggest that peaks in canopy disturbance (albeit minor) only weakly coincided with peaks in recruitment. Work by Tardif and Bergeron (1999) indicates that *F. nigra* regeneration and recruitment are strongly influenced by flooding, perhaps more so than by canopy gaps. In *F. nigra* stands in our study region, woody vegetation typically has shallow root systems (often <30 cm depth; Slesak et al. 2014) to avoid anaerobic conditions resulting from high water tables. The shallow rooting systems render vegetation susceptible to desiccation and mortality during late summer draw-down of the water table. However, excessive moisture also poses a mortality risk to *F. nigra* seedlings, despite the species' tolerance to saturated soil conditions (Tardif et al. 1994). Thus, successful regeneration and recruitment may occur during several consecutive years in which the water table is neither excessively high nor excessively low. Prolonged flooding and prolonged soil drought are the primary causes of *F. nigra* tree mortality in these lowland conditions (Minnesota Department of Natural Resources 2021); we suggest they similarly regulate successful regeneration and recruitment.

Unfortunately, we were not able to test the coincidence of water table fluctuations and *F. nigra* recruitment. Although metrics such as monthly precipitation and regional stream gauge data are available, they provide rather crude proxies for water table fluctuations at the local site scale. Despite these data limitations, we speculate that water table fluctuations and canopy disturbance interact to regulate *F. nigra* regeneration and recruitment in these stands. Given appropriate water table conditions, *F. nigra* likely forms banks of advance regeneration that may benefit from individual- or multiple-tree canopy openings. Indeed, the Minnesota Department of Natural Resources (2021) states that *F. nigra* is unequaled in its ability to maintain sapling banks, likely due to adaptations that allow established seedlings and saplings to persist under flooded conditions (Tardif et al. 1994), as well as the ability to endure low-light conditions (Springer and Dech 2021). Our finding that 61% of trees currently in the canopy achieved canopy status without showing a growth release suggests that this advance regeneration may benefit from but not be entirely dependent on canopy openings.

4.3. Management implications

The pending arrival of EAB in the Great Lakes region will likely result in mortality rates of overstory *F. nigra* much higher than the historical canopy disturbance rates we observed at these sites, and it will likely elevate water tables, as has been confirmed in experimental manipulations (Slesak et al. 2014; Diamond et al. 2018). The excessive flooding associated with EAB mortality may prevent successful regeneration and recruitment of *F. nigra* and other tree species, with the likely conversion to wetland shrub communities (Palik et al. 2021*a*). Climate change predictions for the region point to both increased overall precipitation and longer drought periods (Pryor et al. 2014), as well as shift in precipitation seasonality (Handler et al. 2014), all of which, when combined with loss of *F. nigra* overstory, could further confound the recovery of these sites to forested conditions (D'Amato et al. 2018; Kolka et al. 2018).

Results from this study can nevertheless inform strategies for transitioning these forests to non-EAB-host tree species and those that are future climate adapted. Given the likelihood of widespread *F. nigra* mortality in this region, appropriate management strategies would include underplanting or direct seeding with non-ash tree species to maintain the current hydrologic regime and perpetuate forest cover in these systems (Palik et al. 2021*a*, 2021*b*). We detected no historical analog for the extensive canopy disturbance generated by proposed pre-salvage harvests of *F. nigra* stands in anticipation of this introduced insect. Instead, strategies designed to increase resilience to EAB should build upon the stand histories characterized herein, namely long-term canopy ascension under a canopy-gap disturbance regime. Such strategies would rely on uneven-aged silvicultural prescriptions (through periodic partial canopy removal) and avoidance of stand-replacing disturbances. Similarly, Springer and Dech (2021) recommend single-tree or group selection to emulate the outcomes of natural disturbance and foster regeneration in *F. nigra* stands. Such strategies would maintain hydrologic regimes that may allow for periodic establishment of tree regeneration and recruitment. Related research has demonstrated that this level of disturbance maintains site hydrology in patterns that are indistinguishable from mature, undisturbed forest (Slesak et al. 2014; Diamond et al. 2018).

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The data described in the manuscript will be freely available upon request from the corresponding author.

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Competing interests

The authors declare there are no competing interests.

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