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Stand Dynamics and Structure of Two Primary Champlain Valley Clayplain Forests, Vermont

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Abstract - Understanding natural forest dynamics is critical for informing forest restoration and conservation efforts. However, such information is often difficult to generate for areas that have a long history of intense land use, such as the Champlain Valley of Vermont. We used dendroecological methods and assessments of forest structural conditions to describe the tree recruitment history and structural dynamics of 2 examples of valley clayplain forest, a rare natural community that has been drastically reduced in extent by agricultural land use in the Champlain Valley. Although historic selective harvesting had occurred in the areas sampled, these sites represent the best remaining examples of semi-natural valley clayplain forests in the region, thus providing an opportunity to document long-term patterns of structural and compositional conditions and tree recruitment in areas with limited land-use. Age structures in these 2 areas were strongly uneven-aged, with older cohorts composed of *Quercus alba* (White Oak), including an individual dating to the 1640s, and recruitment over the past 2 centuries dominated by *Tsuga canadensis* (Eastern Hemlock). Size distributions of live trees also reflected these patterns of recruitment, with White Oak occurring exclusively in larger diameter classes (>35 cm) and Eastern Hemlock predominating across all smaller size classes. We observed sparse regeneration of *Quercus* spp. (oaks) in these areas, suggesting that this historically important component of valley clayplain forests may disappear over time in the absence of large, stand-scale natural disturbances or management activities focused on the perpetuation of this species group.

Introduction

An understanding of natural forest stand dynamics is critical for informing ecologically sound forest-management actions (Franklin et al. 2007, Frelich 2002, Oliver and Larson 1990). Studies of stand dynamics can explain how disturbances and species interactions drive forest structure and recruitment patterns of tree species (Spies 1998). Information on factors such as tree establishment dates can be used to better understand the historical processes and patterns of a forest (D'Amato et al. 2006, 2008; Pederson et al. 2013). In addition, this information can be used to predict how a forest might respond to future disturbances, including those related to climate change, invasive species establishment, and forest management activities.

It is difficult to generate an understanding of stand dynamics and successional trends of forests in areas that have a long history of intense land use (Foster et al. 1998, Lapin 2003, Russel Southgate and Thompson 2014, Sprugel 1991). Forest fragmentation and land uses such as logging and grazing can drastically alter forest composition, structure, and successional trends (Russel Southgate and Thompson

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2014, Sprugel 1991). Despite these changes, examining forest stand dynamics in fragmented landscapes remains an important area of research because fragmented forests may still provide carbon-uptake benefits (Reinmann and Hutyra 2017), and they can represent important ecological communities, have cultural value, and be of great significance for guiding ecological restoration of the broader landscape (Lapin 2003). Fragmented forests with long histories of human land-use represent much of the forests in the northeastern US.

The structure and composition of New England forests have been shaped by past land use, particularly historic forest-clearing for agriculture followed by reforestation (Cronon 1983, Foster et al. 1998). In areas of New England that have fertile soils suitable for agriculture, ecological transformation of the landscape has been more acute and permanent with limited recovery of previously forested conditions. One such example is the Champlain Valley of Vermont, which has been heavily cleared and farmed since Europeans moved there in the late 1700s (Hemenway 1867, Siccama 1971). Historically, mixed hardwood–conifer forests, called valley clayplain forests and which grew in the rich clay soils near the shores of Lake Champlain, were a dominant feature of this landscape. The extent of these forests has been drastically reduced by increased human population and agriculture in the area over the past 2 centuries, with these forests now existing in a matrix of small patches across the region. Only 10% of the original area covered by clayplain forest is now forested, and much of this remaining forest is in early-successional stages (Lapin 2003).

The valley clayplain forest is classified as a rare natural community in Vermont due to both the influence of land use on these forests and the regionally unique biophysical settings in which it occurs (Thompson and Sorenson 2000). This natural community is known to host 28 rare or uncommon herbaceous plant species, including 5 endangered and threatened species, and contains tree species that are less common throughout the rest of northern New England and New York, including *Quercus alba* L. (White Oak; Lapin 1998, 2003). Given the rarity of the valley clayplain forest, particularly in relation to its historic abundance, there is increasing interest in restoring this forest type on agricultural lands and other lands on which it historically occurred (Lapin 2003). Previous studies have examined the early successional trends, species composition, classification, and description of this forest type throughout its range (Lapin 1998, 2003; Otsuka 2004). To date, no historical ecological research has been published for Champlain Valley clayplain forests, and tree-species dynamics of late-successional clayplain forest remain largely unknown, particularly the dynamics related to tree recruitment and forest structure (Lapin 2003).

The objective of this study was to fill key knowledge gaps regarding historic patterns of tree recruitment, structural conditions characterizing these forests, and associated implications for restoration efforts (Lapin 2003). We used dendroecological methods and assessments of forest structural conditions to describe the tree recruitment history and structural dynamics of 2 Champlain Valley clayplain forest stands. The first objective of the study was to use tree, seedling, and coarse woody debris data to quantify current structural and compositional conditions of 2 late-successional Champlain Valley clayplain forest stands. The second objective was to determine the tree recruitment history of these 2 sites to draw conclusions about long-term species interactions with disturbance and the successional trajectory of the forest. We expected structural conditions and recruitment dynamics to be consistent with those observed for other oak–mixed hardwood forests in northeastern North America, with recent recruitment reflecting an increase in shade-tolerant species and a concomitant shift away from oak-dominated conditions (e.g., Lorimer 1993, Orwig et al. 2001, Zaczek et al. 2002). Insights gained from these characterizations are intended to guide conservation efforts focused on restoring and maintaining these forest types across the broader Champlain Valley landscape.

Field-site Description

The study took place in 2 forests in the Champlain Valley region of Vermont—Williams Woods in Charlotte, VT and Church Woods in Shelburne, VT (Fig. 1). We chose these 2 sites because they had previously been identified as some of the best remaining examples of late-successional valley clayplain forest patches in the Champlain Valley (Lapin 2001, The Nature Conservancy 2010). Today, clayplain forests exist in small fragments throughout the Champlain Valley, and much of these are in early-successional stages (Lapin 2003, Otsuka 2004). At 25 ha and 15 ha, respectively, Williams Woods and Church Woods are 2 of the largest

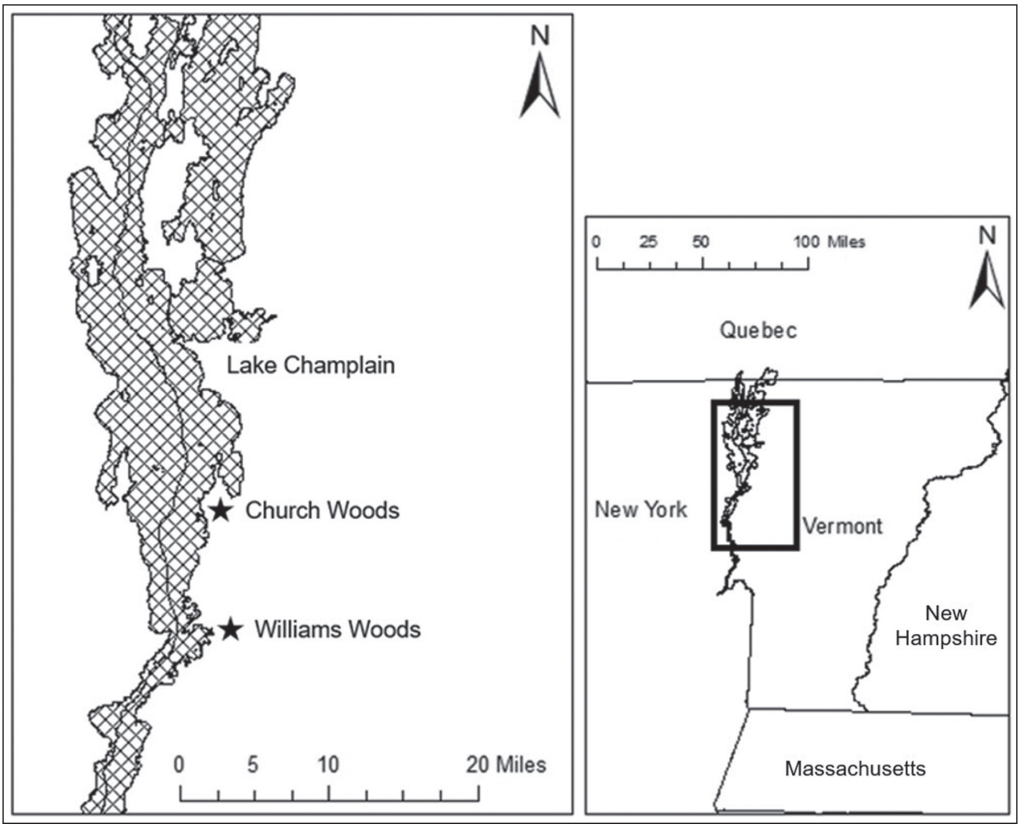

Figure 1. Locations of Church Woods and Williams Woods, VT.

remaining fragments of clayplain forest in the state of Vermont (Lapin 2001, The Nature Conservancy 2010). In addition to their size, these 2 forests were of interest to us because of the advanced age of individual trees on site and species composition. In particular, both forests contain large White Oak individuals that were hypothesized to be over 200 y old in previous reports (Lapin 2001, The Nature Conservancy 2010). Studying these trees was of particular interest because oaks are a defining species group of valley clayplain forests and are uncommon elsewhere in Vermont. Field evidence and historic records suggested that neither site was ever completely cleared for agriculture. Selective harvesting occurred in Church Woods over the 19th and 20th centuries, as evidenced by scattered cut stumps and confirmed through discussions with local managers (M. Webb, Shelburne Farms, Shelburne, VT, and E. Tapper, Vermont Forests, Parks, and Recreation, Essex, VT, pers. comm.). Selective harvesting was also likely done at Williams Woods in the 19th and early 20th centuries; the property was donated to The Nature Conservancy in 1996 (The Nature Conservancy 2010). Despite this history of land use, the areas sampled are recognized as the oldest remaining valley clayplain forests in the state and provided a unique opportunity to reconstruct historic tree dynamics and describe the structure and composition of semi-natural, primary forest examples of this rare forest type. For this work, we defined "primary forest" as areas that were never converted to a non-forest condition by historical land-use (Peterken 1996).

Methods

Plot design

We established one 0.25-ha plot at each of the 2 sites for collecting vegetation and dendrochronological data. We chose a square plot design for ease of mapping tree locations and to minimize edge corrections in the calculation of spatial statistics. Each 0.25-ha plot had nine 2-m–radius regeneration plots spaced 12.5 m apart, and eight 25-m transects radiating from the center for measuring coarse woody debris (CWD). At each site, we placed plots in representative areas of the larger stand that exhibited valley clayplain forest characteristics, including a mixture of *Quercus* (oak), *Tsuga canadensis* (L.) Carrière (Eastern Hemlock), and other hardwood species. Presence of overstory oak species was an important criterion for plot location because the recruitment history of these trees was of specific interest. We recognize that the use of a single plot may have limited our ability to fully capture the range of variation in recruitment and structure across a given site; however, this sampling design has proven effective at describing local spatial patterns of cohort structure in other forest systems (Gill et al. 2015).

Field methods

In each plot, we used an (x, y) coordinate system to map each tree larger than 10 cm in diameter at breast height (DBH; 1.3 m above the ground). We recorded the species, diameter, and crown class of each tree. We grouped trees into 4 crown classes based on Oliver and Larson (1990). In total, we measured 242 and 224 trees at Williams Woods and Church Woods, respectively. We collected an increment core at ~30 cm above the ground from each tree >10 cm DBH rooted within each plot. To capture the age range of this species, we cored 4 additional White Oak individuals, in close proximity to the plot at Williams Woods, that exhibited bark and crown characteristics of older trees. We tallied seedlings and saplings in the 2-m radius regeneration plots. For this study, we considered seedlings to be all individual tree stems shorter than breast height and saplings to be all individual stems taller than breast height and <10 cm DBH. We also collected species presence/absence data for each regeneration plot to determine regeneration stocking across each 0.25-ha plot. We measured CWD in each 0.25-ha plot using the line–intersect method (van Wagner 1968). On each transect, we recorded the diameter, species, orientation, and decay class for each piece of downed CWD >6 cm diameter and >1 m in length encountered along the transect. We determined decay classes based on the 5 classes described in Woodall and Williams (2005). We calculated volume of CWD based on the formula described by van Wagner (1968).

Lab methods

In the lab, we mounted, sanded to 800 grit, and counted the rings on each increment core under a microscope to determine the approximate age of each tree. We used pith indicators based on inner curvature to estimate the establishment date for cores that did not reach the pith of the tree (Applequist 1958). We excluded from reconstructions of age distribution all cores that did not reach the inner curvature of the tree. In total, we included 228 and 205 cores for Williams Woods and Church Woods, respectively. We employed the list method, which records years of irregular growth such as narrow rings in each core to visually crossdate (Yamaguchi 1991), and thus, improve our estimates of tree age. We estimated, but did not confirm, tree age because, for some species, there could be significant error in dating without accounting for missing rings (Lorimer et al. 1999).

We calculated importance values (IV) for each tree species based on relative basal area (m²/ha) and relative density after Curtis and McIntosh (1951). We determined the shape of the distribution of each DBH class for live trees using the methods outlined by Janowiak et al. (2008). In short, this method involves using polynomial regressions in which the base-10 logarithm of each 5-cm DBH class is regressed against various combinations of DBH, DBH^2, and DBH^3, with the best-approximating model selected based on the corrected Akaike information criterion ($\mathrm{AIC_C}$). We used the significance and sign of regression parameters from the best-approximating model to assign a curve form based on Janowiak et al. (2008). We employed the Ripley's K function to determine spatial patterns of live trees based on (x, y) coordinates (Stoyan and Stoyan 1994). We used the function to determine whether trees in different species and cohort groups were dispersed, clumped, or randomly distributed. In our analyses, we ran the L-function, which is a square-root transformation of the K-function that stabilizes its variance and equals zero under complete spatial randomness. We calculated 999 Monte Carlo simulation envelopes to test for deviations from complete spatial randomness using a 95% confidence level. We conducted both the diameter-distribution curves and the spatial statistics in R (R Core Team 2017).

Results

Species composition and stand structure

Williams Woods. The forest at Williams Woods was strongly dominated by Eastern Hemlock (IV = 0.60), which was present in every crown class of the canopy but was most numerous in the smaller DBH classes—below 30 cm (Fig. 2a). The 2 next most-important trees, *Acer rubrum* L. (Red Maple; IV = 0.08) and White Oak (IV = 0.08) were mostly located in the dominant and co-dominant canopy-crown classes (Fig. 3a). We found *Pinus strobus* L. (Eastern White Pine; IV = 0.07) in every crown class of the canopy. The 5th most important tree was *Betula lenta* L. (Black Birch; IV = 0.05), and most individuals of this species were 10–15 cm DBH (Fig. 2a). The *Betula alleghaniensis* Britt. (Yellow Birch; IV = 0.03) surveyed were in the intermediate and codominant crown classes, with DBHs of 25–45 cm (Figs. 2a, 3a). *Fagus grandifolia* Ehrh. (American Beech; IV = 0.02) and *Fraxinus nigra* Marshall (Black Ash; IV = 0.01) occurred in the lower canopy crown classes (Fig 3a). We classified tree species with a count of less than 5 stems as "other" species. These species are *Carya ovata* (Mill.) K. Koch (Shagbark Hickory), *Quercus rubra* L. (Red Oak), and *Acer saccharum* Marshall (Sugar Maple). Spatial analysis of stem locations indicated that the distribution of Eastern Hemlock and other species was completely spatially random at all distances (Fig. 4a). The diameter distribution for Williams Woods (Fig. 2a) was best described by a negative exponential curve (AIC_C = 5.85).

Red Maple was the most numerous and widespread seedling species documented in the Williams Woods regeneration plot (Table 1) with over 20,000 stems/ha and

Table 1. Seedling (all stems shorter than 1.37 m) and sapling (all stems <10 cm DBH and taller than 1.37 m) data from Williams Woods in Charlotte, VT, and Church Woods in Shelburne, VT. Regeneration was measured both in terms of stems per hectare and stocking. Stocking is based on presence or absence in each of the 9 regeneration plots.

	Williams Woods				Church Woods			
Species	Seedl. /ha	Stock.	Sapl. /ha	Stock.	Seedl. /ha	Stock.	Sapl. /ha	Stock.
Acer rubrum (Red Maple)	20,071	89%	0	0%	88	11%	0	0%
Tsuga canadensis (Eastern Hemlock)	88	11%	531	44%	177	11%	88	11%
Fagus grandifolia (American Beech)	265	22%	177	22%	1945	33%	796	22%
Fraxinus pennsylvanica (Green Ash)	177	11%	88	22%	88	11%	0	0%
Acer saccharum (Sugar Maple)	177	22%	0	0%	2210	89%	88	11%
Quercus rubra (Red Oak)	177	22%	0	0%	-	-	-	-
Carya cordiformis (Bitternut Hickory)	88	11%	0	0%	-	-	-	-
Betula alleghaniensis (Yellow Birch)	442	44%	707	22%	-	-	-	-
Quercus alba (White Oak)	442	22%	0	0%	-	-	-	-
Fraxinus nigra (Black Ash)	265	11%	0	0%	-	-	-	-
Pinus strobus (White Pine)	531	22%	0	0%	-	-	-	-
Amelanchier arborea (Michx. F.) Fernald (Common Serviceberry)	-	-	-	-	0%	0	88	11%
Lonicera spp. (honeysuckle)	-	-	-	-	442	22%	0	0%
Betula lenta (Black Birch)	-	-	-	-	3714	22%	0	0%
Rhamnus cathartica (Common Buckthorn)	-	-	-	-	265	22%	531	11%

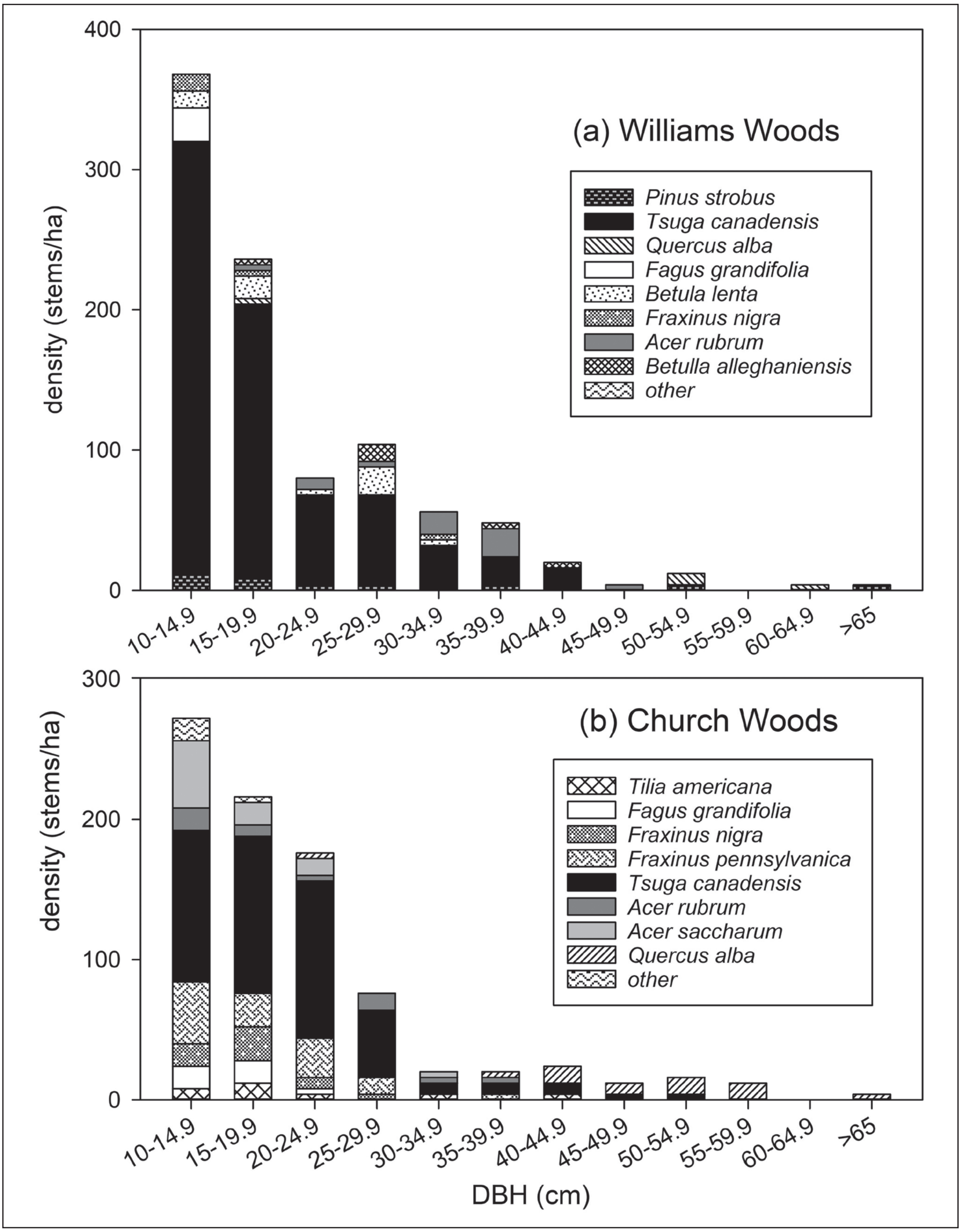

Figure 2. Tree DBH distributions for (a) Williams Woods in Charlotte, VT, and (b) Church Woods at Shelburne Farms in Shelburne, VT. "Other" species in Williams Woods include *Carya ovata* (Shagbark Hickory), *Tilia Americana* (American Basswood)*, Fraxinus pennsylvanica* (Green Ash)*, Quercus rubra* (Red Oak), and *Acer saccharum* (Sugar Maple). "Other" species in Church Woods include *Ulmus Americana* (American Elm), *Carya cordiformis* (Bitternut Hickory), *Rhamnus cathartica* (Common Buckthorn), *Betula papyrifera* (White Birch), *Betula lenta* (Black Birch), *Ostrya virginiana* (American Hophornbeam), *Acer platanoides* (Norway Maple), and *Carya ovata* (Shagbark Hickory).

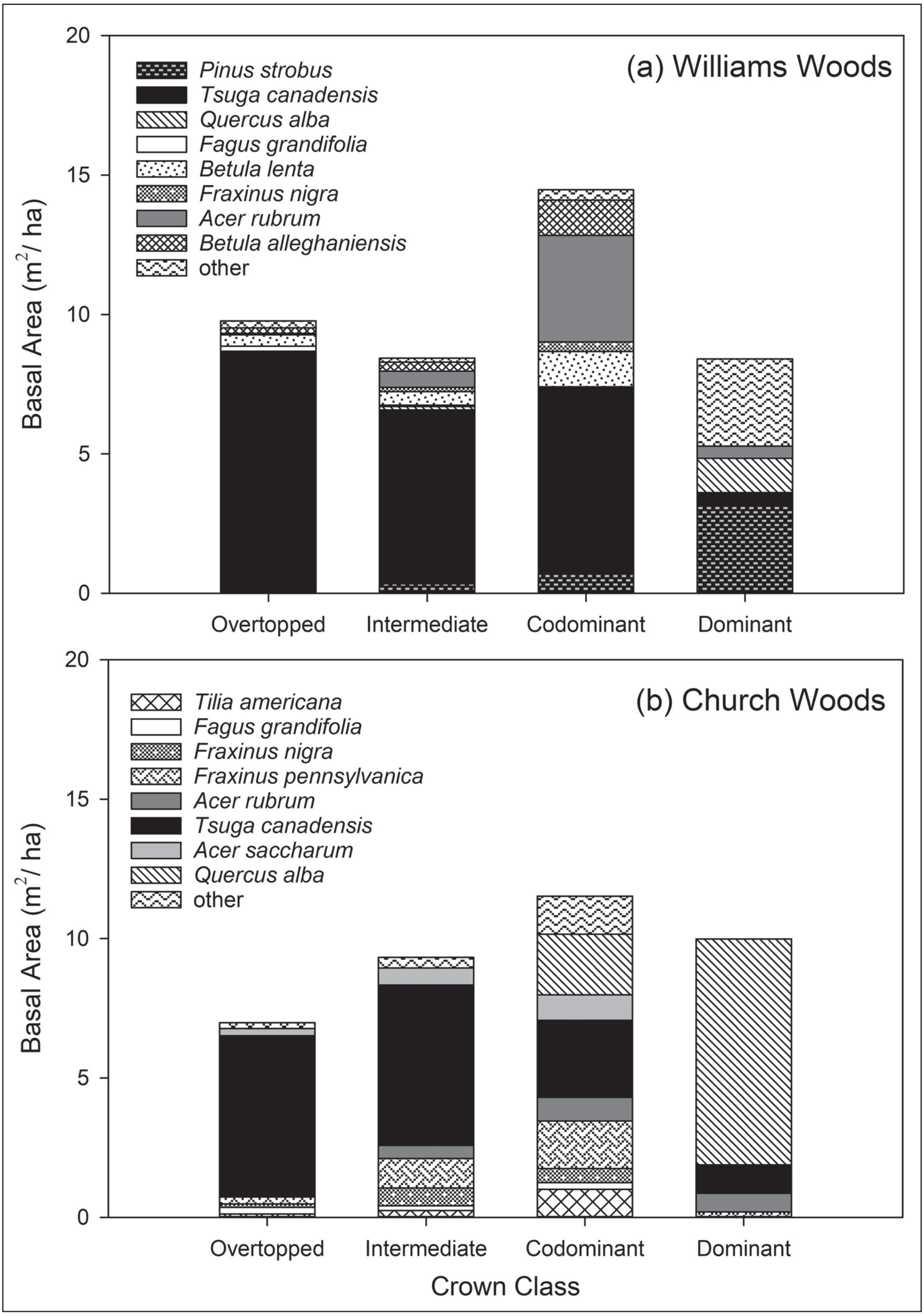

Figure 3. Basal area of canopy tree species by crown class in (a) Williams Woods in Charlotte, VT, and (b) Church Woods in Shelburne, VT. See Figure 2 for species contained in "other" category.

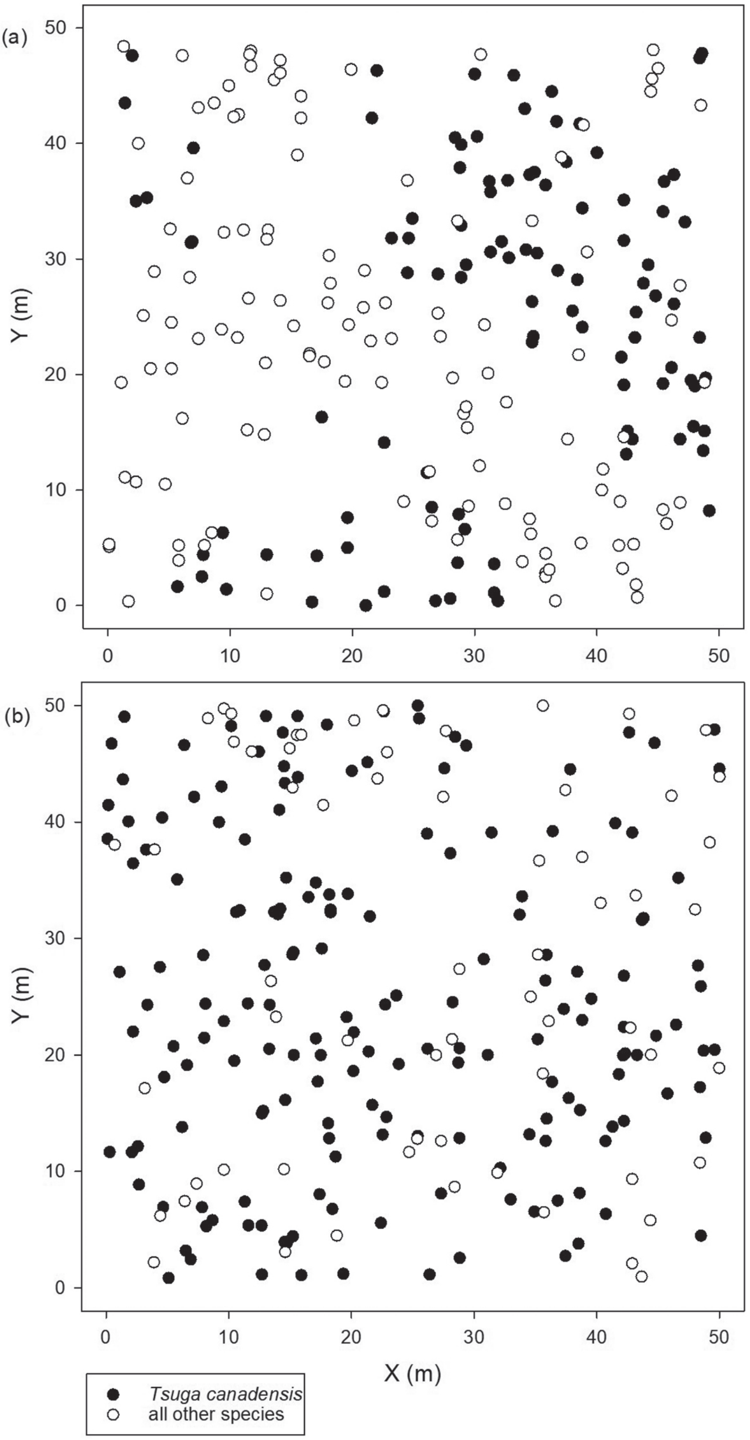

Figure 4. Map of living trees at (a) Williams Woods in Charlotte, VT, and (b) Church Woods in Shelburne, VT.

89% stocking (i.e., percentage of regeneration plots with at least 1 individual). The other most common seedling species were Yellow Birch with 44% stocking and 442 stems/ha and Eastern White Pine with 22% stocking and 531 stems/ha. Red Oak and White Oak both had 22% stocking across the site. Only 1 species, *Carya cordiformis* (Wangenh.) K. Koch (Bitternut Hickory), had seedling presence (88 stems/ha and 11% stocking) but was not reported as present in the overstory. Yellow Birch was the most numerous sapling species (707 stems/ha), and Eastern Hemlock had the highest stocking of saplings (44%). The total volume of CWD at Williams Woods was 77.85 m^3/ha. A larger portion of this CWD was from hardwood species in advanced stages of decay (decay classes 4 and 5; Fig. 5a). Softwood CWD was less common and was concentrated primarily in the least decayed classes (decay classes I and II; Fig. 5a).

Church Woods. Eastern Hemlock was also the most dominant species at Church Woods (IV = 0.43). Other important species were White Oak (IV = 0.17) and *Fraxinus pennsylvanica* (Green Ash, IV = 0.11). Eastern Hemlock and Green Ash trees were mostly smaller than 30 cm DBH and located in the lower 3 crown classes, with a few individuals of larger DBH present in the plot (Figs. 2b, 3b). We only found White Oak trees that were in codominant and dominant crown classes and had DBHs larger than 30 cm (Figs. 2b, 3b). Red Maple, Sugar Maple, *Tilia americana* L. (American Basswood), and American Beech were also abundant in the smaller DBH classes (Fig. 2b). Less-frequent species (less than 5 stems) were *Ulmus americana* L. (American Elm), Bitternut Hickory, *Rhamnus cathartica* L. (Common Buckthorn), *Betula papyrifera* Marshall (Paper Birch), Black Birch, *Ostrya virginiana* (Mill.) K.Koch (Hophornbeam), *Acer platanoides* L. (Norway Maple), and Shagbark Hickory. Individuals of these species were all smaller than 25 cm DBH (Fig. 2b). Spatial analysis of stem location showed significant clumping of Eastern Hemlock at distances of 2–20 m and clumping of all other tree species at 3–15 m (Fig. 4b). The DBH distribution for Church Woods was best explained by a negative exponential curve (AIC_C =15.85).

The most widespread seedling species at Church Woods was Sugar Maple at 89% stocking (Table 1). The most abundant seedling species was Black Birch with 3714 seedlings/ha. American Beech also had a widespread presence in the plot with 33% stocking and 1945 stems/ha. Common Buckthorn and *Lonicera* spp. (honeysuckles) were also present in the regeneration layer. Saplings were primarily American Beech and Common Buckthorn (Table 1). Coarse woody debris volume at Church Woods was 48.62 m^3/ha. Most of this material was hardwood CWD in decay classes 3, 4, and 5, with softwood CWD found in low volumes across decay classes 2–5 (Fig. 5b) .

Age structure

Williams Woods. The forest at Williams Woods was uneven-aged with several distinct recruitment periods (Fig. 6a). The oldest cohort established between 1790 and 1839. However, 2 White Oaks, established in 1640 and 1712, predated this cohort. A second cohort established between 1840 and 1899 and was primarily

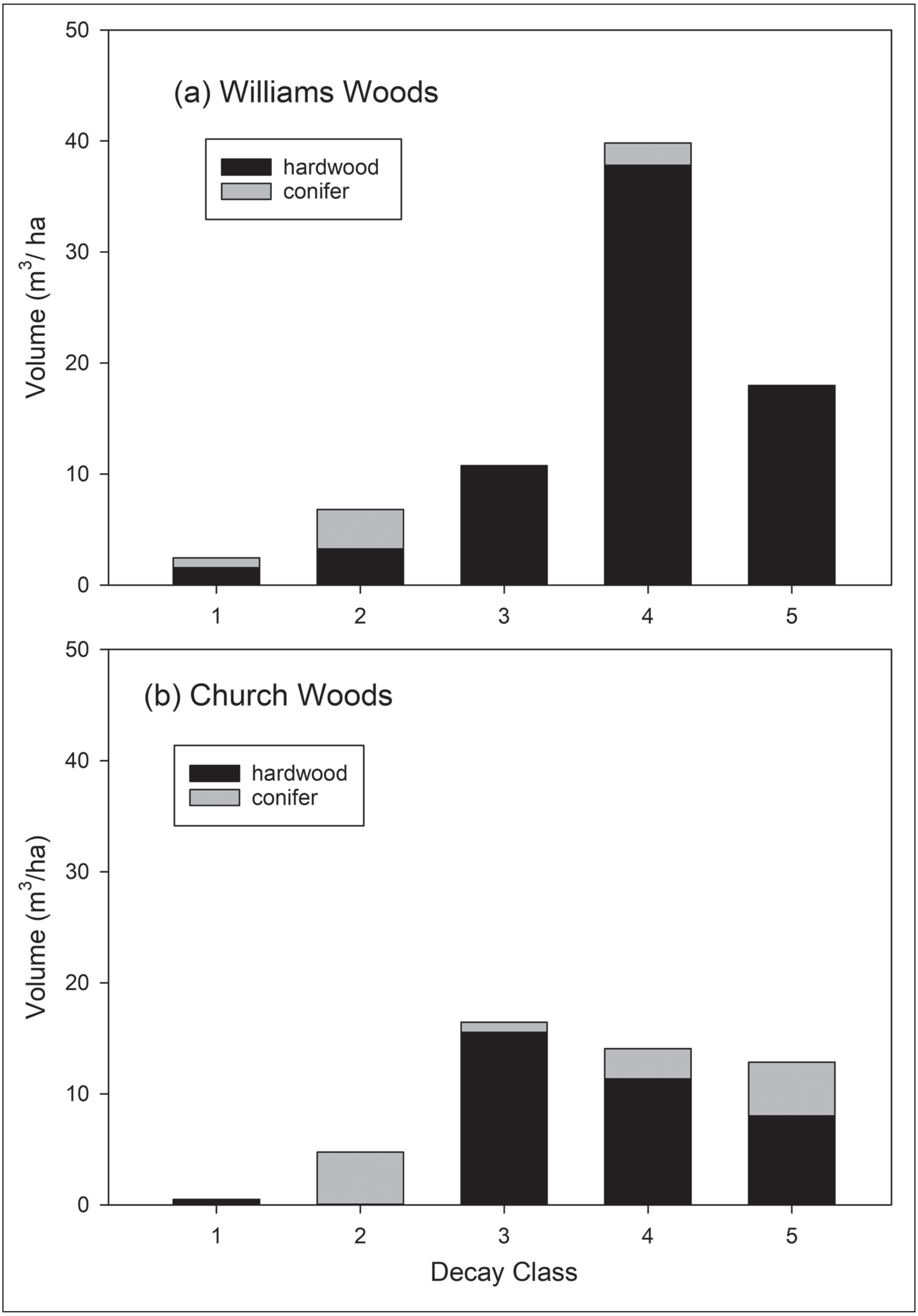

Figure 5. Volume (m³/ha) of course woody debris present in (a) Williams Woods in Charlotte, VT, and (b) Church Woods at Shelburne Farms in Shelburne, VT, grouped by decay class.

dominated by Eastern Hemlock as well as most of the Red Maples, Black Birches, and Eastern White Pines present in the plot (Fig. 6a). The youngest cohort, established between 1900 and 1990, consisted mostly of Eastern Hemlocks. Most of the Yellow Birches present in the plot were recruited between 1930 and 1960,

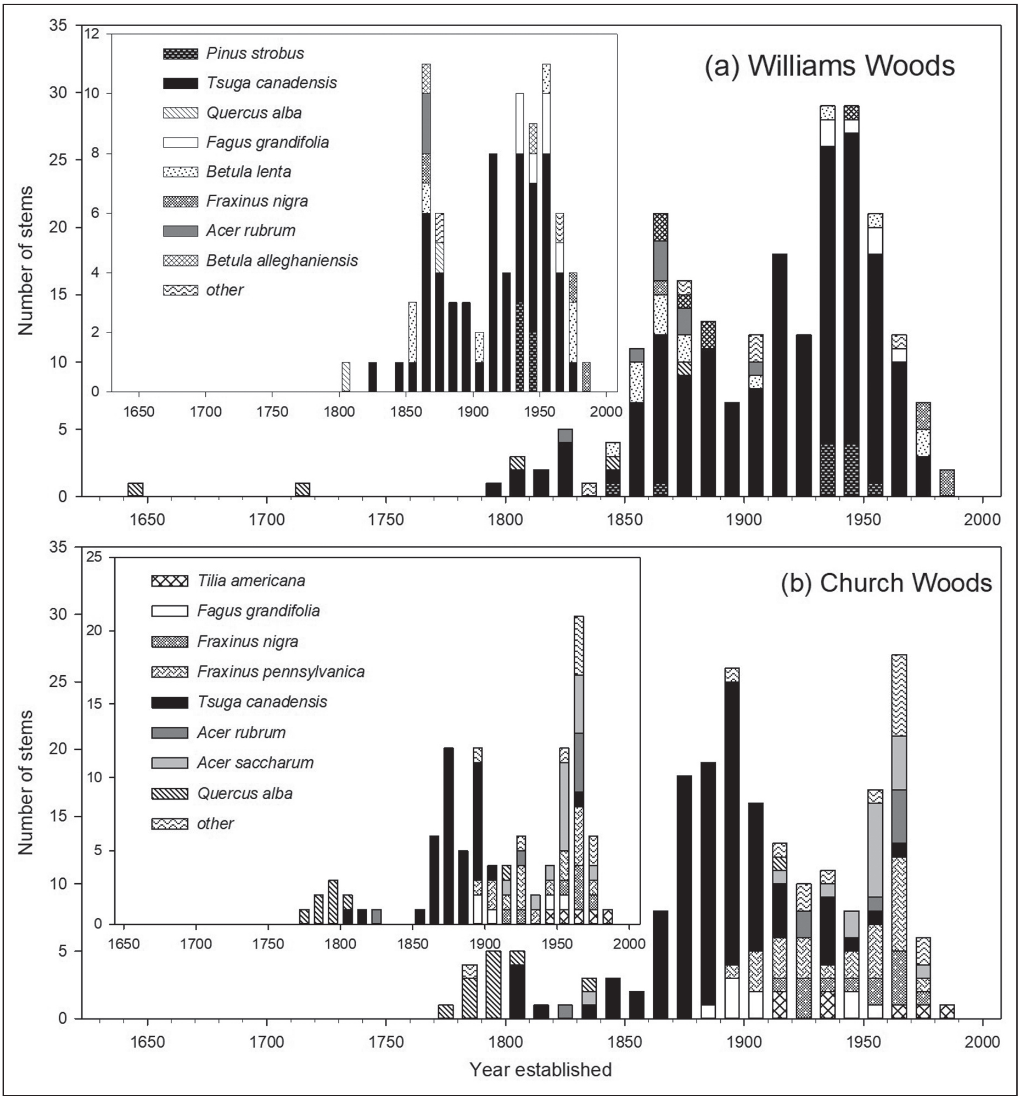

Figure 6. Establishment dates for trees in (a) Williams Woods in Charlotte, VT, and (b) Church Woods at Shelburne Farms in Shelburne, VT. Insets represent subset of core samples that reached pith or were estimated to be 5 years or less from the pith. "Other" species in Williams Woods include *Carya ovata* (Shagbark Hickory), *Quercus rubra* (Red Oak), and *Acer saccharum* (Sugar Maple). "Other" species in Church Woods include *Ulmus americana* (American Elm), *Carya cordiformis* (Bitternut Hickory), *Rhamnus cathartica* (Common Buckthorn), *Betula papyrifera* (White Birch), *Betula lenta* (Black Birch), *Ostrya virginiana* (American Hophornbeam), *Acer platanoides* (Norway Maple), and *Carya ovata* (Shagbark Hickory).

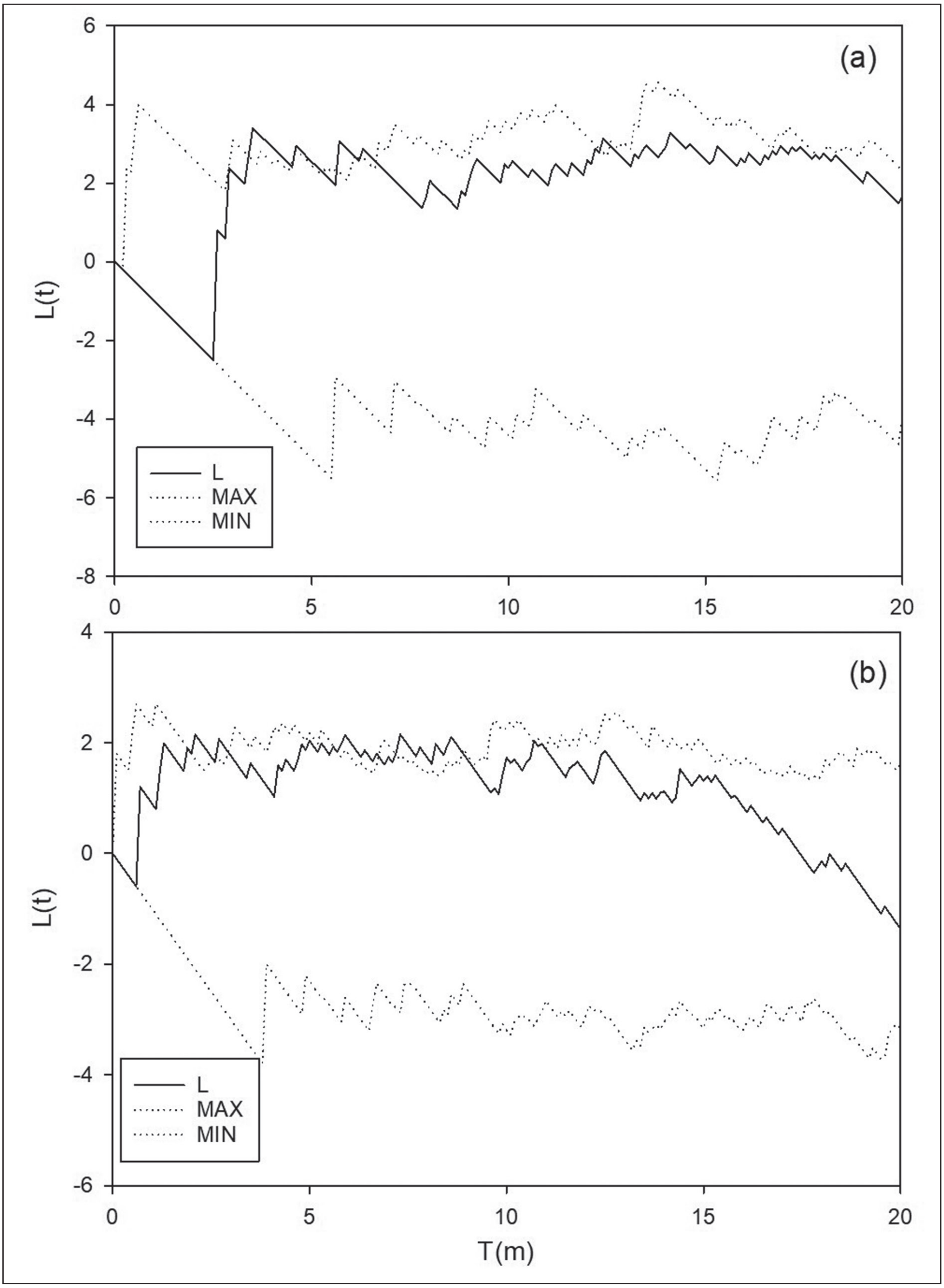

Figure 7. Spatial point patterns for cohorts established in the (a) 1930s and 1940s at Williams Woods, VT, and (b) 1960s at Church Woods, VT. The dark continuous line represents the variance-stabilized Ripley's K-function (L-function) and dashed lines represent 95% confidence envelope for complete spatial randomness hypothesis. Values above the confidence envelope indicate clustering and values below indicate regularity.

and an older generation of this species established around 1850 (Fig. 6a). Most of the Black Ash trees present established after 1970, with a few individuals establishing between 1860 and 1870. Removing from our analysis trees with cores that we estimated to be more than 5 y from the pith did not substantially change the age-structure results, but accentuated the recruitment events in the 1860s, and 1930s–1950s (Fig. 6a). Analysis of spatial distribution of trees grouped by these age cohorts indicated that cohort distribution was spatially random. However, spatial analysis of only trees with cores reaching 5 y and closer to the pith (Fig. 6a) indicated that there was significant clumping of trees that established in the 1930s and 1940s at distances between 3 m and 6 m (Fig. 7a).

Church Woods. The forest at Church Woods was also uneven-aged with 3 distinct cohorts (Fig. 6b). The oldest cohort consisted mostly of White Oaks and established between 1780 and 1810. A second pulse of recruitment occurred between 1860 and 1920, when most of the Eastern Hemlocks in the plot established. The most recent, distinct recruitment event was mixed hardwood establishment from 1940 to 1990, with a peak between 1960 and 1970. Most of the non-oak hardwoods in the plot were established during this time. Removal from our analysis of trees with cores that we estimated to be more than 5 y from the pith did not substantially change the age-structure results, but highlighted the increase in tree recruitment in the 1870s, 1890s, 1960s, and 1970s. Spatial analysis of trees with cores estimated to be 5 y or less from the pith (Fig. 6b) showed that trees established in the 1960s were significantly clumped at 5–10 m (Fig. 7b).

Discussion

Quercus dynamics

Both study sites contained scattered oak trees in the overstory, and Williams Woods had limited White Oak and Red Oak seedlings in the plot. However, no oaks were present in the lower crown classes of the canopy at either site, and there were no oaks present in either plot established after 1875. Instead, the overtopped and intermediate crown classes were dominated by Eastern Hemlock, Yellow Birch, Red Maple, and American Beech, indicating a long-term shift from oak dominance to those late-successional species. This successional trend away from oak has been recorded extensively in recent decades throughout the temperate forests of the eastern US (Frelich and Reich 2002, Knopp 2012, Lorimer 1993, Orwig et al. 2001, Zaczek et al. 2002). Evidence from those previous studies suggests that large disturbances, such as fires, that historically favored oak regeneration no longer occur in contemporary landscapes. Without these disturbances, shade-tolerant species begin to predominate as small-scale disturbances generate conditions more favorable for their establishment (Buchanan and Hart 2012, Knopp, 2012, Lorimer 1993, Zacek et al. 2002); thus, Frelich and Reich (2002) listed wind disturbance as one of the 3 main threats to old-growth oaks in fragmented ecosystems, given that these events do not create canopy gaps large enough for oak regeneration to successfully recruit into the overstory (Frelich and Reich 2002). Past studies of clayplain forests have identified localized wind events and ice storms as the main disturbances affecting contemporary clayplain forest ecosystems (Lapin 2003), which may explain the lack of recent oak recruitment into the sapling layer and overstory crown classes observed in this study. Deer browse has also been identified as a factor limiting oak recruitment (Rodewald 2003); however, we did not find evidence of extensive deer browsing within the study area. Finally, changes in land use over time may also explain the trend away from oak in late-successional clayplain forests. In particular, the 2 study sites were likely used as open-canopy grazing woodlots when oaks established (late 1700s and early 1800s), which would have provided the open conditions necessary for oak to successfully recruit.

One question that remains regarding the valley clayplain forest is what processes originally led to the establishment of oaks on these sites. Records and evidence from our data show that oak was present in these forests before Europeans moved into the area. Fire is thought of as the preeminent driver of oak regeneration (Johnson et al. 2009), and studies from central New England indicated that old-growth oak–hickory forests were present in areas that have a higher fire occurrence than the surrounding areas (Orwig et al. 2001). It was previously thought that fire was not a common disturbance in the Champlain Valley (Lapin 2003); however, historic burning by the Abenaki tribe in this region may have encouraged and maintained oak dominance in these areas (Cogbill et al. 2002, Cronon 1983, Siccama 1971).

Structural and compositional conditions

The dominance of Eastern Hemlock in the 2 sites we examined reflects a lack of historic agricultural clearing, as this species rarely dominates areas with a history of agricultural land use (D'Amato et al. 2008, Foster et al. 1998). At Williams Woods, Black Birch and Yellow Birch were also abundant, which is consistent with other work in the region that has highlighted these 2 species as common components of old-growth Eastern Hemlock forests (D'Amato et al. 2006). The high frequency of CWD and historic windthrows at Williams Woods likely provided ideal environments for Yellow Birch regeneration; this species regenerates on downed logs, particularly those of Eastern Hemlock, and on exposed mineral soil (Marx and Walters 2008).

Eastern Hemlock also dominated the Church Woods site; however, there was a significant hardwood component that included several species associated with wet forest conditions such as Black Ash, Green Ash, and Red Maple. The tree spatial patterns at this site indicated significant clumping and likely reflected an underlying environmental gradient in the plot, as there was a wetter portion of the stand in the southwestern corner that contained a high number of hardwood species associated with lowland areas. This result is consistent with past observations of clayplain forest communities that documented significant shifts in species composition over short distances due to slight changes in underlying soil drainage (Lapin 2003).

We detected the invasive species Norway Maple, Common Buckthorn, and honeysuckle at Church Woods. The presence of invasive species such as Common Buckthorn and honeysuckle has been recognized as one of the 3 main threats to old-growth oak communities in fragmented landscapes (Frelich and Reich 2002). The presence of these species in Church Woods represents a significant challenge to future maintenance of the ecological conditions in this area.

Previous studies of forests similar in composition to valley clayplain forest have not measured CWD (Buchanan and Hart 2012, Knopp 2012, Zaczek et al. 2002). The volume of CWD we documented fell between amounts recorded for other types of oak- and hemlock-dominated forests in the eastern US (D'Amato et al. 2008, Goebel and Hix 1996, Wilson and McComb 2005). This pattern likely reflects the transition from detrital inputs dominated by hardwood species towards the more decay-resistant Eastern Hemlock, as oak becomes a lesser component over time and Eastern Hemlock ascends into dominant canopy positions. The difference in CWD volumes at Williams Woods and Church Woods is likely due to a difference in land-use history between the 2 sites, such as a more recent clearing in Church Woods, and a recent large wind disturbance in 2007 at Williams Woods that blew down many overstory trees (The Nature Conservancy 2010).

Recruitment history

As has been demonstrated for much of New England (Cronon 1983, Foster et al. 1998), land-use history can influence forest composition, structure, and long-term forest dynamics. Evidence from this study suggests that land use was the driving factor for recruitment events in both forests, despite their general characterization as old-growth forest remnants. Before this study, the oldest tree in Williams Woods was estimated to be 285 y old (The Nature Conservancy 2010); however, we cored 2 White Oak trees in Williams Woods, established in 1640 and 1712, that predate Europeans moving to the Champlain Valley. Although there were some Europeans present in the Champlain Valley before the signing of the Treaty of Paris in 1783, it was after this event that European population increased substantially (Hemenway 1867). Local experts believe that most trees were felled in the area during that period and that even the oldest stands in the valley are mostly second growth, with oaks sprouting from the original old-growth trees that were felled at that time (M. Lapin, Middlebury College, Middlebury, VT, pers. comm.).

The 2 oldest trees at Williams Woods displayed an initial period of suppression in the late 1700s and early 1800s (H. Murray, unpubl. data), which reflects recruitment under a tree canopy (Frelich 2002) and indicates that this area was never completely cleared of trees. However, both cores showed evidence of a release event in the early to mid-1800s, a potential response to selective logging of trees in the area by farms adjacent to this fragment (Beers 1869). Grazing was also a common practice in farm woodlots during that time, and the cessation of grazing as farms were abandoned or converted to other agricultural uses may have contributed to a change in species composition and to increasing recruitment during this period (Cronon 1983, Foster et al. 1998).

Natural disturbances and drought have also likely played a role in the recruitment history at Williams Woods. The recruitment event documented between 1810 and 1840 corresponds with an 1815 hurricane that may have contributed to gap formation favoring advance regeneration of shade-tolerant species (Orwig et al. 2001). The recruitment event documented between 1930 and 1960 overlapped with the 1938 hurricane and with the 1960s drought, the most severe drought in New England over the last century (Pederson et al. 2013). Given the shallow rooting-depth in these forests, overstory trees are quite susceptible to wind disturbance and to moisture stress, and those 2 events likely contributed to the recruitment event observed over this period. The significant clumping of trees that established in the 1930s and 1940s supports the idea that gaps were created in the 1938 hurricane, allowing successful recruitment of groups of trees. Given the decay rates for oak CWD (Russell et al. 2014), the amount of hardwood CWD in decay class 4 at Williams Woods also may be the result of these past events. There has not been a stand-replacing disturbance at Williams Woods since Europeans arrived in the Champlain Valley (Lapin 2003), but the largest documented disturbance in recent history was a large wind event in 2007 (The Nature Conservancy 2010). Trees that established or recruited after this event were too small at the time of the study to extract increment cores but were evident by the abundance of Yellow Birch in the regeneration layer.

Most of the recruitment patterns documented at Church Woods were directly or indirectly related to human disturbance. This record includes a heavier and more recent history of logging than at Williams Woods, with the last harvest occurring in 1975 and 1976 (E. Tapper, pers. comm.). The first continuous European population in Shelburne was established in 1784 (Hemenway 1867), a time period corresponding with the establishment of White Oak at Church Woods. Anecdotal accounts indicate that the area was forested at the time of purchase in 1886 (E. Tapper and M. Webb, pers. comm.); given its location at the corner of 4 different farms, it was most likely used as a grazing woodland in the early 1800s.

A selective timber harvest in 1976 at Church Woods has had a large impact on recruitment of hardwood species in this forest. During this harvest, 118 m^3 of Eastern White Pine and assorted hardwood species were harvested from the site (E. Tapper, pers. comm.). This harvest released advance hardwood regeneration and led to the recruitment of other hardwood species, including American Basswood and Black Ash. Harvest records from this event indicate that numerous overstory Sugar Maple, American Beech, and White Oak were removed, with this composition matching descriptions of pre-settlement vegetation for the area (Cogbill 2002, Siccama 1971). The significant clumping of trees that established during the 1960s and the diverse group of species in that age cohort suggests that mixed hardwoods in the understory were released into the canopy after trees were removed in the 1976 harvest.

Conclusion

Prior to this study, little was known about the dynamics and development of present-day valley clayplain forests (Lapin 2003). Descriptions based on field observations have emphasized the dominance of oaks, Green Ash, Eastern White Pine, and hickories, and a projected successional trajectory of this community toward overstory dominance of Eastern Hemlock in addition to oak, hickory, and ash species (Lapin 1998, 2003; The Nature Conservancy 2010, Thompson and Sorenson 2000). Our results confirm the general pattern of Eastern Hemlock as a late-successional species in these systems and provide greater detail about the recruitment dynamics of this and other constituent species. Although oak is often described as a defining feature of these forests (Cogbill et al. 2002; Lapin 1998, 2003; The Nature Conservancy 2010), the lack of recent recruitment of these species and the advanced age of the individuals already present indicate that those species may not be sustained over time. If oak is a desired future component of these forests, deliberate management actions may be required to encourage regeneration and subsequent recruitment into the canopy. This activity may include removing the understory of shade-tolerant species in places to promote oak regeneration (Lorimer 1993).

Our results indicate that the valley clayplain forest has a species composition and recruitment history that have been heavily influenced by human land-use throughout the past 225 y. Current species composition in these areas indicates that tree species present in the clayplain forest are variable and that there is no one stable condition that can describe a typical clayplain forest. However, the valley clayplain forest contains unique tree species assemblages that managers, landowners, and conservation organizations might want to preserve. Evidence from our study suggests that regeneration of late-successional species will happen naturally despite forest fragmentation, but a large threat to valley clayplain forest systems is invasive species, many of which were present in large concentrations at Church Woods. Invasive species such as Norway Maple and Common Buckthorn could alter natural recruitment dynamics of native tree species characterizing valley clayplain forests and should be aggressively managed in areas where clayplain forest restoration is a goal.

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