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ORIGINAL PAPER

Characterizing northern white-cedar communities in harvested and unharvested lowland forests of Michigan, USA

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Abstract Understanding the complexity of forest community dynamics is essential in forest management planning and stewardship, yet lowland northern white-cedar (*Thuja occidentalis* L.) are often managed as homogenous communities. Through this study, we defined lowland white-cedar forest community types in unharvested and harvested forest stands within the State of Michigan and examined community type associations with ecological variables. Data collected in unharvested stands revealed three white-cedar community subtypes: (1) cedar-deciduous, (2) cedar-conifer, and (3) cedar-shrub. These unharvested subtypes were dominated by white-cedar, yet characterized by different soils, hydrology, geochemical gradients, and associated tree species. In harvested stands, six community types were identified: (1) aspen-fir, (2) winterberry-willow, (3) balsam fir, (4) cedar-red maple, (5) cedar-black spruce, and (6) alder-tamarack. These harvested community types were located along ecological gradients, including soil type (organic or mineral) and soil water pH. Using community types in unharvested and harvested stands, and associated ecological gradients, potential pathways of compositional transition were theorized. Findings suggest that cedar community subtype affects the likelihood of cedar regeneration and dictates the alternative species replacing cedar after harvest. These findings and potential pathways are useful to forestry practitioners, as they highlight potential changes in tree species dominance following harvest across a range of lowland white-cedar community types, allowing refinement of silvicultural prescriptions to ensure desired outcomes.

Keywords Northern white-cedar · Forested wetland · Community typing · Forest management

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Introduction

Northern white-cedar (white-cedar; *Thuja occidentalis* L.) is an archetypal tree species in the northern Great Lakes region and beyond. Endemic to North America, white-cedars grow in diverse lowland, upland, and transitional forest communities.They are slow- to moderate-growing conifers, which live for hundreds to over one thousand years (Johnston 1990; Kelly et al. 1994). White-cedars' present range spans southeastern Canada and the north-central and northeastern United States, with a southwestern border that crosses the Laurentian mixed forests of the Lake States (Johnston 1990; Faber-Langendoen 2001). This range includes cool, humid climates with a relatively short growing season and the majority of annual precipitation occurring during the cold season (Johnston 1990).

Across their range, white-cedars have high phenotypic plasticity and are found growing across a spectrum of ecological gradients (Briand et al. 1992). They function both as late-successional and long-lived pioneer species in forest stand development. White-cedars have been classed as very shade tolerant, tolerant, and intermediate, depending on growth strategy and site (Curtis 1946; Johnston 1990). White-cedars typically grow on organic and mineral soils with a pH of 5.5 to 7.2 (Curtis 1946). They often dominate in forested fens with flowing, mineral-rich groundwater and peat thicknesses of 0.3 to 1.8 m (Johnston 1990). They reproduce by seed and by layering, which may occur under low light conditions. Climate, hydrology, soils and soil chemistry, and associate flora are essential factors in white-cedar habitat on fens, bogs, other wetlands, as well as upland sites (Chimner and Hart 1996; Curtis 1946; Johnston 1990).

White-cedars maintain important roles in these communities, with unique relationships with hydrology and above- and below-ground flora and fauna. White-cedars create essential wetland components of summer and wintering habitat for white-tailed deer (Odocoileus virginianus), snowshoe hare (Lepus americanus), and other boreal transition plants and wildlife (Doepker and Ozoga 1991; Storm and Kenefic 2022; Ullrey et al. 1967). White-cedars also provide medicines, teachings, and materials for humans, including timber and non-timber forest products in small- and large-scale industries (Boulfroy et al. 2012; Clark et al. 2022). Despite their importance, white-cedars have been one of the least studied commercially important tree species in North America (Boulfroy et al. 2012).

Just three centuries ago in the northern Great Lakes region, white-cedar communities grew within large expanses of intact forest stewarded by Indigenous peoples. White-cedar forest communities were populated with large trees, surpassing 50 cm in diameter (Willis in Clark 2021, Johnston 1990). Many of these large-diameter trees were removed by colonial settler logging and fire in the mid-nineteenth to mid-twentieth centuries. After a period of rapid regeneration (Heitzman et al. 1997), white-cedars have since declined in abundance across their range (Cornett et al. 2000a; Danneyrolles et al. 2017; Dupuis et al. 2011; Hofmeyer et al. 2009).

Declines in white-cedar populations have been attributed to changing land tenure, forest and land management, and associated changes in hydrology and herbivory (Boulfroy et al. 2012; Cornett et al. 2000b; Danneyrolles et al. 2017; Dupuis et al. 2011; Heitzman et al. 1997; Hofmeyer et al. 2009). Timber production, forest conversion, and infrastructure development directly remove white-cedars from the landscape, and have been found to alter long-term, local hydrologies to their detriment (Chimner and Hart 1996; Chimner et al. 2017). Silvicultural strategies for both white-cedar and non-cedar species have been associated with reduced white-cedar regeneration and recruitment, as well as replacement by associates such as alder (*Alnus incana* L.), balsam fir (*Abies balsamea* (L.) P. Mill), and red maple (*Acer rubrum* L.) (Nelson 1950; Thornton 1957; Chimner and Hart 1996; Heitzman et al. 1997). In fact, many agencies consider white-cedar stands as no management areas to avoid losing white-cedars from the landscape through active management.

Mature white-cedars can withstand centuries of change, yet recent failures in regeneration and recruitment have prompted concerns about the continuity of white-cedar populations and associated forest communities. White-cedar dominated forests are projected to decline in the future due to climate-driven change that is expected to compound and amplify existing stressors (Handler et al. 2014; Iverson et al. 2008, 2016; Peters et al. 2020; Matthews et al. 2011). Given past, present, and projected future changes, it is important to understand the diverse plant communities in which white-cedars grow, community types in harvested white-cedar forests, and their relationships with ecological gradients on the landscape. This information can help inform forest stewardship and the call by Boulfroy et al. (2012) for silvicultural prescriptions that explicitly address white-cedar.

White-cedars have been categorized according to several ecological community and habitat typing systems across their range. These typing systems identify assemblages of plants and other organisms sharing common habitat to understand a site, its processes, history and potential future states. Vegetation-based classification systems rely on observable patterns of plant communities, which include dominant and/or diagnostic species, and are understood to integrate environmental conditions, ecological processes, and biogeographical dynamics of a site (Faber-Langendoen 2001). Habitat classification systems include succession-based (e.g., Burger and Kotar 2003), existing vegetation-based (e.g., Eyre 1980), and other complex systems that consider community origins, disturbance histories, and dynamic ecosystem processes (Faber-Langendoen 2001; Grossman et al. 1998). These typing systems span fine to coarse scale resolutions, requiring managers to select from among broad- to fine-scale community types. In forest management, habitat classification is important to establishing long-term stand goals and developing treatment prescriptions to reach those goals.

For white-cedars, approaches to classification vary. For example, lowland white-cedar forests have been managed as one broad forest type: SAF type 37 (Eyre 1980; Thornton 1997), and as several lowland types: lowland cedar, mixed coniferous lowland forest, and lowland deciduous with cedar, among others (MDNR 2013). The *Silvicultural Guide for Northern White-Cedar* includes two lowland white-cedar types according to soils and hydrology: deep, moist mineral soils and deep, very moist mineral or organic soils (Boulfroy et al. 2012). These forest types offer important frameworks for managing and sustaining white-cedar into the future. A premise of basing harvest treatments on classification is that the treatment will maintain or develop the classified type. Yet, classifications do not directly address white-cedar response to silvicultural treatment. Thus, a greater understanding of how habitat classification and forest composition stabilize or change treatment is needed to develop management alternatives to maintain and support white-cedars in future forests.

The objectives of this study were to: (1) characterize white-cedar community types and ecological gradients in unharvested (no known harvest history) forested wetlands across Michigan and (2) characterize white-cedar swamp communities post-harvest to determine if regenerating communities match or deviate from unharvested communities. We hypothesize that unharvested white-cedar swamps are not one community type, but several spanning hydrologic and soil gradients. We hypothesize that post-harvest white-cedar community types will track the pre-harvest community types. Our overall goal is to better understand natural white-cedar community characteristics and their relationships with ecological gradients and if these gradients influence forest regeneration after harvest. This information will be relevant to developing management options to recover and sustain white-cedar forests into the future.

Methods

The study occurred in two phases. Phase I took place in Michigan's eastern Upper Peninsula during years 1 and 2 and involved assessments of unharvested plots on tribal, federal, and state forests. In year 3, Phase II expanded the study to include paired harvested and unharvested plots, as well as additional unharvested plots, across the State of Michigan on state, federal, and tribal lands. The study area is located near the southern boundary of white-cedar's natural range (Little 1971). The climate is moderated by three Great Lakes: Superior, Huron, and Michigan and characterized by cool summers and winters with moderate to high snow depth, depending on proximity to each Great Lake. Study area soils range from excessively drained mineral to very poorly drained organic, as well as thin calcareous soils along the Niagara escarpment.

Site selection

This study focused on lowland white-cedar in forested wetlands, so we only analyzed plots that were classified as wetlands within National Wetlands Inventory (USFWS 2000). Field data collection was conducted over several years and broken into two phases of data collection. Phase I occurred in the eastern Upper Peninsula of Michigan and Phase II expanded the collection to all of Michigan, each with slightly different methods due to different objectives of ancillary studies. Data collected through each phase have combined and harmonized for consistency in the analysis and interpretation.

For Phase I, we used LANDFIRE Existing Vegetation Type (EVT) ecological systems (LANDFIRE 2014) to establish field assessment plots within the eastern Upper Peninsula of Michigan. The EVTs are based on NatureServe's Ecological Systems classification, U.S. National Vegetation Classification alliances, the National Land Cover Database and additional types, and mapped using decision tree models that combine Landsat imagery, field, elevation, and biophysical data. Field assessment plots were selected from two EVT systems, which include white-cedar as a dominant or co-dominant species: Laurentian-Acadian Alkaline Conifer-Hardwood Swamp Shrubland (3281) and Forest (3481). A two-hectare hexagonal grid was overlaid on the EVT systems across four land-tenure types: tribal, state (including forest and wildlife management areas), federal forest lands, and federally designated Wilderness Areas and Research Natural Areas. Grid cells with 75% or more coverage of the EVT systems and located completely within the boundaries of each land tenure type were selected. Plots were assigned to hexagonal grid cell centroids, stratified by land tenure type, in a generalized random-tessellation stratified design (Stevens and Olsen 2004). Thirty sample plots were identified on each of tribal, federal forest, and state land tenure types. Ten sample plots were identified on federally designated wilderness and research natural areas, as reference areas with limited silvicultural management over the last century.

Phase II assessed harvested white-cedar stands identified by Michigan Department of Natural Resources, adjacent unharvested "parent" white-cedar forest, and unharvested stands on federal lands across the Upper and northern Lower Peninsulas of Michigan. Harvested stands had undergone silvicultural treatments (e.g. clearcut, strip, patch, and partial cut) between 10 and 67 years prior to assessment. Field assessment plots were randomly established ex-situ using ArcGIS 10, with a minimum 20-m buffer from stand edges. We sampled 1 plot per 4 ha of harvested area with a minimum of 3 plots and maximum of 6 plots per treated stand. Additionally, unharvested "parent" stand plots were established in-situ, adjacent to harvested areas with a 20-m buffer from the harvested area and from stand edges.

Data collection

Field sites were visited over the course of three summers during the 2019–2021 field seasons. Complete field data were collected at 377 plots on 147 stands: 23 tribal forest plots (14 stands), 300 state plots (104 stands), 34 federal plots (25 stands), and four federal wilderness plots (4 stands). Plot sizes and certain field methods differed slightly among the two phases of the study (Fig. 2).

In Phase I, overstory and understory structure and composition, microtopography, soils, and herbivory were assessed using 10-m radius (plot) and 2.1-m radius (subplot) circular nested plots with radial transects (Fig. 2). At plot center, canopy closure was recorded as percent closure using two hemispheric photographs taken with a fisheye lens (Sony A6300; 7Artisans 7.5 mm), analyzed with Gap Light Analyzer (Frazer et al. 1999), and averaged for each plot. Within the 10-m radius plot, species and diameter at 1.37 m above the ground (D) were measured and recorded for all live and standing dead trees 12.7 cm D and greater. Microtopography and coarse woody material (CWM) were measured using the line-intercept method along three 10 m radial transects within the plot beginning in a random direction from plot center and at 120-degree intervals. Incremental lengths of microtopography were recorded as hummock (raised areas over 0.2 m in height), lawn (comparatively flat areas), and pool (visible surface water or depressions indicating water table presence at or above the soil surface during the growing season [Chimner and Hart 1996]). Coarse woody material (2.5 cm in diameter and larger) species, diameter at intercept, and five classes of decay (1: freshly fallen, 2: sound with bark slippage, 3: heartwood sound with outer decay, 4: heartwood rotten, and 5: collapsed) were recorded along each transect.

Within the 2.1-m radius subplot, woody stems less than 12.7 cm D were tallied by species and height class (< 5 cm, 5-30.4 cm, 30.5–91.4 cm, 91.5 cm-1.4 m, 1.5-3 m, and > 3 m). Unknown species were photographed and identified ex-situ. Percent of bryophyte ground cover was recorded as 5 ordinal classes (0%, 1–25%, 26–50%, 51–75%, and 76–100%) and analyzed by midpoints.

Phase II plots were assessed using 11.3-m (large), 5.6-m (medium), and 0.8-m (small) radius circular nested plots with radial transects (Fig. 2). At the plot center, canopy percent closure was measured using CANOPYAPP 1.0.3 (UNH Earth Systems Research Center) at 2-m above ground. Within the 11.3-m radius large plot, species and D were measured and recorded for all live and standing dead trees 15.2 cm D and greater. Microtopography and coarse woody material were measured using the line-intercept method along three 11.3-m radial transects within the plot, similar to Phase I.

Within the 5.6-m radius medium plot, species and diameter class of woody stems greater than 2.4 m in height and less than 15.2 cm D were recorded. Diameter classes included individuals less than 4 cm, 4 to 7.9 cm, 8 to 12.6 cm, and 12.7 to 15.2 cm D. Within the 0.8-m radius small plots, seedling species and density were recorded by height classes: less than 0.3 m, 0.3 to 0.9 m, 1 to 1.4 m, and 1.5 to less than 2.4 m height. Percent of bryophyte cover was measured with Phase I methods. In both phases of the study, soil water pH and temperature were measured at or near plot center using a YSI Pro1030 handheld pH meter (Ohio, USA). Where water was not present at the soil surface, field crews dug a narrow soil pit less than 10 cm below the soil surface to take water measurements. Soils were also characterized as either organic (dominated by organic material at least 40 cm below soil surface) or mineral (dominated by mineral material within 40 cm depth).

Data from both study phases were combined and used to calculate harmonized plot-level vegetation characteristics. We created a matrix of plot-level species abundance data in two size classes: density of saplings and small trees greater than 0.3 m height and less than 15.2 cm D, and basal area of large trees 15.2 cm D and larger. Sapling and small tree density and overstory tree basal area values were relativized by maximum to address the difference in plot sizes in the two phases. This matrix was used to assess unharvested and harvested plot community types.

A complete list of plot-level explanatory variables used in this study with descriptive data is included in the Appendix. We calculated plot-level variables for microtopography and structure. Additional vegetation characteristics were calculated, including per hectare stem density (all size classes), relative basal area and relative density of trees 15.2 cm D and greater (relative basal area is the basal area of a given species per hectare divided by the basal area of all species per hectare; relative density is the number of a given species' stems per hectare divided by the number of all species' stems per hectare), and quadratic mean D for white-cedars 15.2 cm D and larger. White-cedar seedling (<0.3 m height) and sapling (≥ 0.3 m height and <12.7 cm D) densities were also calculated for each plot.

We acquired plot-level treatment and ecological variables, including soil type, pH, and climate-related variables. Silvicultural treatment history was provided by Michigan Department of Natural Resources and U.S.D.A. Forest Service. Mean annual snow depth in millimeters (October-March from 2003 to 2019) was determined remotely using ArcGIS 10 (ESRI, National Operational Hydrologic Remote Sensing Center 2004). Latitude and soil drainage class were determined remotely using ArcGIS 10 (ESRI) and elevator, tidyr, and dplyr packages in R version 3.5.0 (R Core Team 2021, Hollister and Shah 2017, Wickham 2021, Wickham et al. 2021). Soil drainage class (SSURGO) is a measure of both the frequency and duration of saturated soil conditions, referring to the processes and conditions of soil development, except where anthropogenic activities have altered soil morphology (USDA 2017).

Data Analysis

Multivariate analyses were performed using PC-ORD version 7.08 (McCune and Mefford 2018). Using our matrix of plot-level species density and basal area data relativized by maximum, we identified unharvested and harvested forest community types through hierarchical agglomerative cluster analysis with Sorenson distances and flexible beta linkages less than or equal to -0.25 (McCune and Mefford 2018). We used indicator species analysis (Dufrêne and Legendre 1997) to identify the species characterizing each cluster and a Monte Carlo analysis to understand the significance ($p<0.05$) of species' indicator values within each cluster. We reviewed the cluster dendrogram, indicator species composition of each cluster, and the average p-values across all species for each cluster level, from two to ten clusters. We selected the cluster levels with the lowest average p-value, highest number of significant indicator species (p-value less than or equal to 0.05), and/or management-relevant break in the cluster dendrogram, hereinafter referred to as community type.

We visually examined our plot-level species data, newly identified community types, and plot-level ecological variables through Multivariate Nonmetric Multidimensional Scaling (NMS). NMS ordinations allow the exploration of plant community relationships with numerous, even highly correlated, ecological variables within synthetic dimensions. We used the autopilot and slow and thorough settings with the Sorensen distance measure to determine statistical significance, based on stress values from 500 runs with real and randomized data. The final number of dimensions was determined by a Monte Carlo test ($p < 0.05$) to minimize stress values (McCune and Mefford 2018). The percent of variance represented by each NMS ordination axis was then calculated from the proportion of the variation in the distance matrix, compared with the variation in the original data matrix. Pearson and Kendall correlation coefficients were calculated for each ecological variable along each NMS ordination axis (McCune and Mefford 2018).

To better understand the differences among community types, we assessed community characteristics, as well as the relationships between community types and ecological variables (see Appendix for full list). We used a one-factor permutational analysis of variance (PerMANOVA) test with bootstrapping to assess differences in composition and relative abundance among the identified unharvested and harvested community types.

Results

Database description

We visited and assessed 377 plots within 154 wetland forest stands across the study area, including 184 plots in unharvested stands and 193 plots in harvested stands. Plots were located across three degrees of latitude (43.76 to 46.89 N) and five degrees of longitude (− 88.51 to − 83.42 W). Mean annual snow depth in millimeters (October-March from 2003 to 2019) ranged from 95.5 to 424.7 mm (mean 244.4, standard deviation 60.8). Summary information for study plots are shared in Table 1.

White-cedar community subtypes in unharvested stands

Hierarchical cluster analysis of the unharvested plot data identified three white-cedar-dominated plant community subtypes: cedar-deciduous wetland, cedar-conifer wetland, and cedar-shrub wetland (Table 2). The most frequently occurring white-cedar community subtype among plots was the cedar-conifer wetland, with 116 plots (63% of unharvested plots). The cedar-shrub wetland subtype was identified in 37 plots (20% of plots) and the cedar-deciduous wetland subtype was identified in 31 plots (17% of plots).

Non-metric Multidimensional Scaling (NMS) analysis of the three unharvested white-cedar community subtypes resulted in a three-dimensional solution obtained through 78 iterations, with a stress of 18.23 and instability of < 0.00001 (Fig. 3; Table 3). The final solution explained 75.8% of the variation in species composition. Axis 1 explained the most variation with an r^2 of 0.317 and was most correlated with basal area per hectare ($r^2 = 0.629$), quadratic mean diameter of white-cedar ($r^2 = 0.247$), white-cedar saplings per hectare ($r^2 = 0.189$), and coarse woody material mean diameter ($r^2 = 0.122$). Axis 2 had an r^2 of 0.286 and was most correlated with soil type ($r^2 = 0.125$) and soil pH ($r^2 = 0.090$). Axis 3 had an r^2 of 0.155 and was most correlated with white-cedar sapling density ($r^2 = 0.071$). Axes and their correlations with the top ecological variables are shown in Table 3.

The cedar-deciduous wetland was dominated by white-cedar and red maple in both basal area and stem density (Table 1). This white-cedar community subtype was more often located on mineral soils (54% of plots) than the other two subtypes in unharvested plots. The cedar-deciduous wetland had the lowest percent hummock and moss cover, lowest relative density of white-cedar, and the highest quadratic mean diameter of white-cedar among community subtypes in unharvested stands (Tables 2 and 4). Soil pH was slightly lower than the other community subtypes (Table 4). Soil drainage in the cedar-deciduous community subtype was spread across four categories: very poorly drained (71.0% of plots), poorly drained (16.1%), somewhat poorly drained (one plot, at 3.2%), and well drained (three plots, at 9.7%).

The cedar-conifer wetland was dominated by white-cedar and black spruce (*Picea mariana* (Mill.) Britton) in basal area, while balsam fir, white-cedar, and red maple were high in stem density (Table 1). This subtype was most often located on organic soils (72% of plots) and had the greatest values for soil pH and basal area for white-cedar among white-cedar community subtypes in unharvested stands (Tables 2 and 4). The cedar-conifer wetland sub-community had the lowest percent microtopography as pool and stem density of grey alder, compared with the other community subtypes in unharvested stands (Tables 2 and 4; Appendix). Soil drainage was very poorly drained (89.7% of plots), poorly drained (4.3%), somewhat poorly drained (3.4%), and included plots with excessively drained soils (3 plots at 2.6%).

The cedar-shrub wetland was dominated by white-cedar and tamarack (*Larix laricina* (Du Roi) K. Koch) in basal area and by white-cedar, alder, and balsam fir in stem density (Table 2). This community subtype was most often located on organic soils (81% of plots) and had the highest values for hummock and pool microtopography, and stem density for white-cedar, alder, and tamarack, compared to the other unharvested community subtypes. The cedar-shrub wetland had the lowest canopy closure, quadratic mean diameter of white-cedar, and basal area per hectare of white-cedar, among the unharvested community types (Tables 2 and 4). Soil drainage was most often very poorly drained (78.4% of plots), with the remaining plots located in poorly and somewhat poorly drained soils (10.8% of plots located in each category).

White-cedar community types in harvested plots

Hierarchical cluster analysis identified six community types within the harvested plot dataset: aspen-fir, winterberry-willow, balsam fir, cedar-red maple, cedar-black spruce, and alder-tamarack (Table 5). The most frequently occurring communities among harvested plots were aspen-fir (23% of harvested plots), balsam fir (21%), and alder-tamarack (21% of harvested plots). The cedar-black spruce community was identified at 32 plots (17%), the winterberry-willow community was identified at 20 plots (10%), and the cedar-red maple community was identified at 15 plots (8% of harvested plots).

Non-metric Multidimensional Scaling analysis of the six community types in harvested plots resulted in a three-dimensional solution obtained through 109 iterations with a stress of 19.1 and instability of <0.00001 (Fig. 4). The final solution explained 58.7% of the variation in species composition. Axis 1 explained the most variation with an r^2 of 0.282 and was most correlated with species richness ($r^2 = 0.076$), mean annual snow depth ($r^2 = 0.065$), and quadratic mean diameter of white-cedar ($r^2 = 0.061$). Axis 2 had an r^2 of 0.173 and was most correlated with quadratic mean diameter of white-cedar ($r^2 = 0.195$), species richness ($r^2 = 0.132$), and canopy closure ($r^2 = 0.1072$). Axis 3 had an r^2 of 0.132 and was most correlated with white-cedar sapling density ($r^2 = 0.041$) and quadratic mean diameter of white-cedar (($r^2 = 0.041$). Axes and their correlations with the top ecological variables are shown in Table 6.

The aspen–fir community was dominated by quaking aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.) in basal area and dominated by balsam fir, mountain maple (*Acer spicatum* Lam.), and balsam poplar in stem density (Table 5). This community type had one of the lowest values for stand age among community types in harvested plots. The aspen-fir community had one of the highest occurrences of mineral soils and lowest soil pH values (mean 6.61) of all harvested community types (Table 4). Soils were most often very poorly drained (77.8% of plots), poorly drained (8.9%), and somewhat poorly drained (13.3%).

The winterberry-willow community was dominated by small-diameter winterberry (*Ilex verticillata* (L.) A. Gray), willow (*Salix* spp.), and paper birch (*Betula papyrifera* Marshall) in stem density (Table 5; Appendix). This community type had the lowest values for canopy closure, moss cover, white-cedar relative density, and white-cedar saplings per hectare (Table 4), and the second lowest values for stand age, among community types in harvested plots. The harvested winterberry-willow community type had one of the highest incidences of organic soils (85% of plots) among community types in harvested plots. Soils were very poorly drained in all plots of this community type (100%).

The balsam fir community was dominated by white-cedar and balsam fir in basal area and dominated by balsam fir in stem density (Table 5). This community type had the highest canopy closure values and the lowest values for hummock microtopography, latitude, and white-cedar seedling density, among community types in harvested plots. The balsam fir community also had one of the lowest relative basal area measures for overstory white-cedar among community types in harvested plots. Plot soils were very poorly drained (95.1% of plots) and somewhat poorly drained (4.9%), while the soil type was most commonly organic (78%).

The cedar-red maple community was dominated by white-cedar and red maple in both basal area and stem density. Black ash (*Fraxinus nigra* Marshall) and paper birch also contributed to plot basal area and stem density values (Table 5; Appendix). This community type had the highest values for coarse woody material diameter and decay class, latitude, pool microtopography, white-cedar tree diameter and relative basal area, and white-cedar seedling density among community types in harvested plots (Table 4; Appendix). Plot soils were very poorly drained (93.3%) and poorly drained (6.7%) and had the highest pH values of all community types (mean of 7.0).

The cedar-black spruce community was dominated by white-cedar and black spruce in basal area and stem density, along with white pine and tamarack (Table 5; Appendix). This community type had the greatest average stand age (38.9 years), hummock microtopography, moss cover, mean annual snow depth, and relative density of white-cedar stems and white-cedar sapling density, among community types in harvested plots. The cedar-black spruce community had one of the lowest values for soil pH (mean of 6.61) and the lowest values for pool microtopography, among community types in harvested plots (Table 6). Plot soils were all very poorly drained (100%).

Finally, the alder-tamarack community type was dominated by alder, wild raisin (*Viburnum cassinoides* L.), and tamarack in stem density and dominated by white-cedar and tamarack in basal area (Tables 4 and 10). This community type had the lowest values for coarse woody material diameter and decay class, and mean diameter and relative basal area of overstory white-cedar trees. The alder-tamarack community type had one of the highest occurrences of organic soils (85% of plots) among community types in harvested plots, as well (Table 4). Soils had moderate pH values (6.72) and were very poorly drained (87.5% of plots), poorly drained (10%), and excessively drained (one plot at 2.5%).

Multivariate plant community analysis of plots in unharvested and harvested white-cedar lowland forest stands identified significant differences (PERMANOVA: $F = 8.7_{8,126}$; $p < 0.01$).

Discussion

Recent declines in white-cedar abundance have been attributed to complex interactions among human land use, forest management, and associated changes in hydrology and herbivory (Boulfroy et al. 2012; Cornett et al. 2000b; Danneyrolles et al. 2017; Dupuis et al. 2011; Heitzman et al. 1997; Hofmeyer et al. 2009). It has been known for decades that timber harvesting is one of the major factors associated with declines in white-cedar and replacement by alder, balsam fir, and red maple associates (Nelson 1950; Thornton 1957, Heitzman et al.1997). Influential factors in the rates of replacement of white-cedar by associate species have been identified to include soils, hydrology, and browse, though detailed guidance on tailoring silvicultural systems to avoid such replacement are lacking.

Composition

In this study, we compared community composition in harvested and unharvested plots and propose possible trajectories in forest composition, with soil type, hydrology, and pre-harvest community composition as predominant influences in forest response to harvest. We found that common associate species (alder, balsam fir, black spruce, and red maple) characterized the lowland white-cedar community types identified through this study, in both unharvested and harvested plots. Community types in harvested plots encompassed a broader range of white-cedar basal area and mean diameter values, with lower average values compared to white-cedar community subtypes in unharvested plots (Table 4).

The majority of our plots in unharvested stands were dominated by white-cedars in the overstory, with a mean relative basal area of 65.7% white-cedar (Appendix). These plots are broadly consistent with the State of Michigan's lowland cedar forest type in both species composition and location on the landscape (MDNR 2013). However, our data indicate that these unharvested white-cedar wetlands are not one community type, but actually 3 subtypes that vary by soil, hydrologic, and geochemical gradients. We named these white-cedar community subtypes: (1) cedar-deciduous wetland, (2) cedar-conifer wetland, and (3) cedar-shrub wetland.

We classified six community types in post-harvested stands, which together had a mean relative basal area of only 36.8% white-cedar (Appendix). These six community types are broadly consistent with current lowland typing systems: lowland mixed deciduous (harvested aspen-fir), lowland mixed conifer (harvested cedar-red maple, cedar-black spruce and balsam fir-alder), and lowland shrub-scrub (harvested winterberry-willow and alder-tamarack) cedar forests (MDNR 2013).

Of the six post-harvest community types, only the cedar-red maple community had white-cedar basal area measures similar to those of unharvested plots (Table 4). This community type formed 7.8% of the harvested plots sampled, meaning that 92.2% of harvested plots had very low white-cedar dominance in overstory basal area. The cedar-black spruce and cedar-red maple community types had high white-cedar seedling and relative density measures, indicating potential future growth in white-cedar dominance; however, these two community types formed 24.4% of the harvested plots sampled, leaving 75.6% of plots in harvested stands with overall low white-cedar dominance. This finding is in line with prior research that has shown that many harvested white-cedar wetlands have not regenerated back to white-cedar, but instead have been replaced by species such as alder, balsam fir and red maple (Nelson 1950, Zasada 1952, Thornton 1957, Heitzman et al. 1997). Many interacting factors (e.g., silvicultural practices, excessive browsing by wildlife, light, hydrology, water chemistry, and competition) affect the regeneration success of white-cedar, with a single limiting factor rarely identified (e.g., Reuling et al. 2019).

Based on our study, we hypothesize that an additional factor, white-cedar community subtype, affects the compositional outcome after disturbance, including the likelihood of white-cedar versus other species regeneration (Fig. 5). Similarly, white-cedar community subtype influences the implementation of the harvest itself, including which species are harvested and how much total timber is removed from the stand. White-cedar community subtype thus influences the range of implemented treatments and regeneration outcomes, thereby contributing to directional change in stand composition.

Based on our results, we propose that, when white-cedar lowlands are harvested, they follow two potential trajectories. They either have successful white-cedar retention and/or regeneration and recover to resemble the unharvested community, or they have poor white-cedar retention and/or regeneration and convert to an alternative community composition (Fig. 5). We suggest that unharvested white-cedar community subtype may help predict what species will likely replace white-cedar if white-cedar is not retained and/or does not regenerate and recruit after timber harvest.

For example, when the cedar-deciduous community subtype is harvested, it may regenerate back to a forest community that resembles the original cedar-deciduous community subtype with high white-cedar basal area, or it may regenerate with less white-cedar and higher proportions of aspen, red maple, and other deciduous trees. Similarly, when a cedar-shrub community subtype is harvested, it may regenerate back to resemble the pre-harvest conditions or shift to increased alder and tamarack dominance. The cedar-conifer wetland community subtype may regenerate back to a similar composition or shift toward less white-cedar and more balsam fir. This concept helps explain findings from the last 80 years of studying white-cedar regeneration (Nelson 1950, Zasada 1952, Thornton 1957, Heitzman et al. 1997).

Factors related to composition

The forest stands assessed in this study tell a more nuanced story of compositional change, where, potential transitions in community composition and characteristics are not straight-forward (Table 4). Important local site conditions associated with white-cedar regeneration and recruitment have been documented in previous studies, including circumneutral to high soil pH (Heitzman et al. 1999, Johnston 1990), hummock microtopography (Cornett et al. 2000b; Palik et al. 2015) on lowland sites (Chimner and Hart 1996; Curtis 1946), moss cover (Holcombe 1976; Lukkarinen 2014), and seed rain from overstory white-cedar trees, with white-cedar basal area as a common metric (Larouche et al. 2011; Reuling et al. 2019; Rooney et al. 2002; Saucier et al. 2018). Our study findings reflected similar associations among white-cedar seedling and sapling densities and site conditions across community types. However, there were differences among plots in unharvested and harvested stands. In unharvested stands, white-cedar seedling and sapling densities were highest in the cedar-shrub community subtype, which was characterized by organic soils, high hummock microtopography and moss cover, and low white-cedar basal area. Among harvested stands, we found that white-cedar seedling

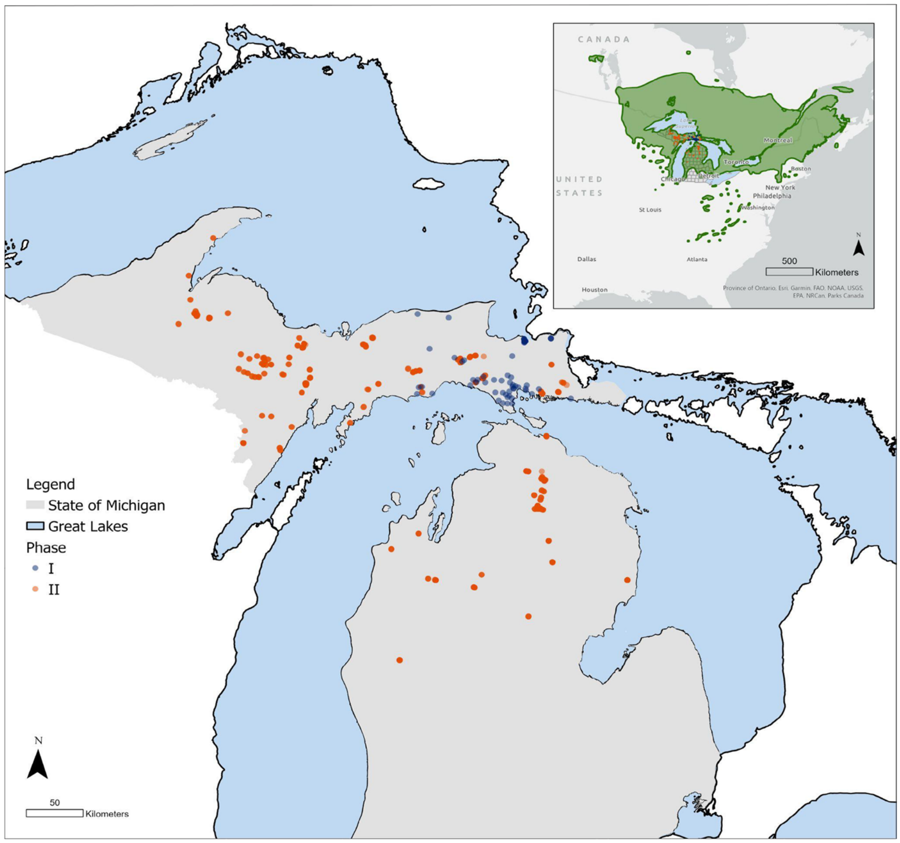

Fig. 1 Field plot locations, including Phase I unharvested sites within the eastern Upper Peninsula of Michigan and Phase II unharvested and harvested, in reference to the range of white-cedar (upper panel) and to the state (lower panel)

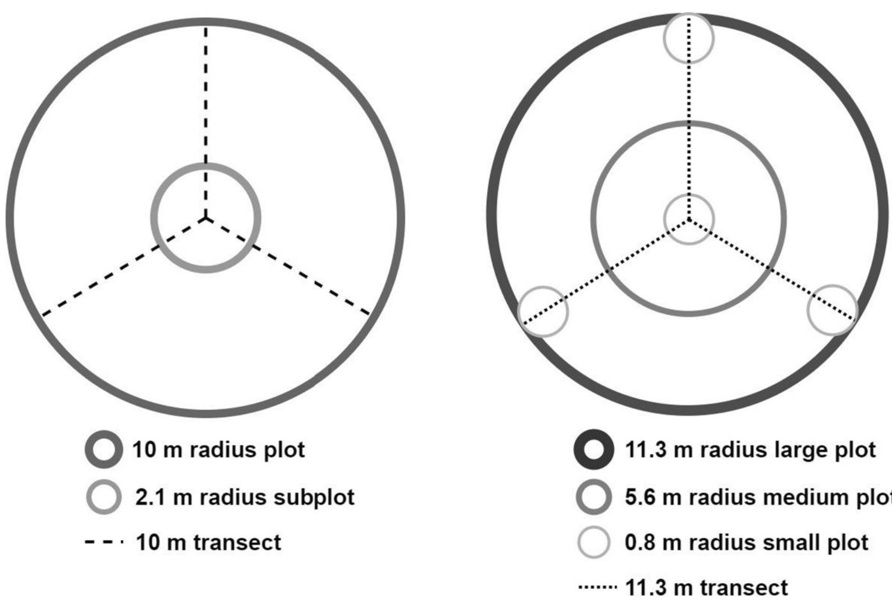

Fig. 2 Field assessment plot design for the two phases of the study: Phase I's nested 2.1-m and 10-m radius plot design with three 10-m radial transects, and Phase II's nested 0.8-m, 5.6-m, and 11.3-m radius plot design with three 11.3-m radial transects

Table 1 Plot-level ecological variables with short descriptions and values for all plots assessed ($n = 377$ plots)

Ecological variable	Variable description	Number of plots (% of all plots)	Mean (range)
Soil type	Soil dominated by organic material at least 40 cm below soil surface	276 (73.2%)	–
	Soil dominated by mineral material within 40 cm below the soil surface	101 (26.8%)	–
Soil pH	Soil water pH measured at soil surface or within 10 cm below the soil surface	–	6.6 (4.0–8.9)
Soil drainage	Very poorly drained soils	330 (87.5%)	–
	Poorly drained soils	23 (6.1%)	–
	Somewhat poorly drained soils	17 (4.5%)	–
	Well drained soils	3 (< 1%)	–
	Somewhat excessively drained soils	1 (< 1%)	–
	Excessively drained soils	3 (< 1%)	–
Hummock microtopography	Percent of microtopography as hummock (areas raised 0.3 m or greater than the surrounding area)	–	17.1 (0–80.0)
Pool microtopography	Percent of microtopography as pool (areas saturated with water during all or part of the growing season)	–	14.0 (0–75.0)
Moss cover	Percent of bryophyte cover analyzed by midpoint of one of 5 ordinal classes: 0%, 1–25%, 26–50%, 51–75%, and 76–100%	–	31.5 (0–88.0)

Table 2 White-cedar wetland plant community subtype (based on Hierarchical Cluster Analysis) dominant species characteristics for 184 plots in unharvested stands. Basal area calculated for trees 15.2 cm D and larger; density calculated for all size classes

Community subtype ($n = 184$)	Dominant species	Common name	Basal area (m^2/ha)	Density (stems/ha)
Cedar- deciduous wetland ($n = 31$)	*Thuja occidentalis* L.	White-cedar	18.77 ± 3	4478 ± 1087
	Acer rubrum L.	Red maple	4.82 ± 0.96	24,055 ± 5039
	Pinus strobus L.	White pine	2.68 ± 1.17	43 ± 38
	Betula alleghaniensis Britt.	Yellow birch	2.46 ± 0.76	966.83 ± 403.85
	Populus tremuloides Michx.	Quaking aspen	1.66 ± 0.78	231 ± 151
	Acer saccharum Marshall	Sugar maple	0.24 ± 0.17	1849 ± 643
	Picea glauca (Moench) Voss	White spruce	0.98 ± 0.45	339.69 ± 175.02
Cedar-conifer wetland ($n = 116$)	*Thuja occidentalis* L.	White-cedar	34.25 ± 1.59	9620 ± 1366
	Picea mariana (Mill.) Britton	Black spruce	3.44 ± 0.44	1431 ± 244
	Abies balsamea (L.) Mill	Balsam fir	0.46 ± 0.07	11,402 ± 1135
	Acer rubrum L.	Red maple	0.51 ± 0.12	8538 ± 1069
	Betula papyrifera Marshall	Paper birch	1.17 ± 0.18	426 ± 152
Cedar-shrub wetland ($n = 37$)	*Thuja occidentalis* L.	White-cedar	13.45 ± 2.24	28,673 ± 5511
	Larix laricina (Du Roi) K. Koch	Tamarack	2.21 ± 0.48	1384 ± 603
	Abies balsamea (L.) Mill	Balsam fir	0.14 ± 0.08	11,175 ± 4074
	Alnus incana (L.) Moench	Grey alder	0 ± 0	9061 ± 2186

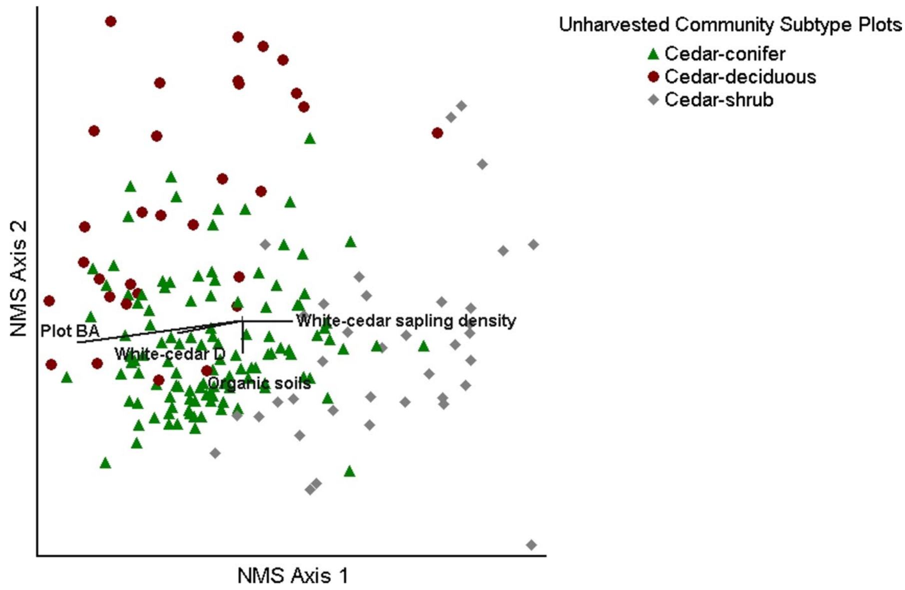

Fig. 3 Non-metric Multidimensional Scaling solution of three white-cedar wetland community subtypes in unharvested plots, with ecological variables with r^2 values greater than 0.125 shown as vectors on axes 1 (31.7% of variance explained) and 2 (28.6% of variance explained), where vector length is proportional to explanatory strength (axis 3 not shown)

Table 3 Top Pearson (r^2) and Kendall ranked (tau) correlations of ecological variables with ordination axes for the NMS analysis of white-cedar community subtypes in unharvested plots, with r^2 values greater than 0.090 on one or more axes

Variable	Axis 1		Axis 2		Axis 3	
	r^2	tau	r^2	tau	r	tau
Total plot basal area	0.629	–0.614	0.082	–0.218	0.04	0.143
White-cedar overstory D	0.247	–0.411	0.047	–0.066	0.035	–0.024
White-cedar sapling density	0.189	0.26	0.003	–0.057	0.071	–0.144
CWM diameter	0.122	–0.199	0.001	0.001	0.003	–0.044
Canopy closure	0.094	–0.187	0.002	0.026	0.021	0.151
Soil pH	0.014	–0.048	0.09	–0.171	0.004	–0.04
Organic soils	0.003	0.036	0.125	–0.264	0.006	–0.058

density was highest in the cedar-red maple community, which had the highest soil pH values among harvested plots, high values for hummock microtopography, more frequent occurrence of mineral soils, and high white-cedar basal area (indicating potential retention of white-cedar overstory through harvest).

We were interested in understanding the relationships between community types and climate, with a focus on latitude and snow depth. The community subtypes in unharvested stands had greater mean values for both latitude and snow depth, reflecting the higher concentration of unharvested plot locations in the northern extent of the study area (see Fig. 1), which is more centrally located within white-cedar's range and characterized by larger expanses of white-cedar forest cover (Peters et al. 2020). In comparison, plots in harvested stands were slightly more often located at lower latitudes, closer to the southern extent of white-cedar's range and in areas characterized by warmer climates and lower snow depth. Importantly, the cedar-deciduous unharvested community subtype had the greatest values for snow depth of all identified communities. This community subtype included tree species indicative of the Boreal Forest community type (Kost et al. 2007), such as yellow birch (*Betula alleghaniensis* Britt.) and white pine (*Pinus strobus* L.), the latter of which had much reduced basal area and density values among plots in harvested stands. This relationship between the cedar-deciduous community subtype and high snow depth indicates that snow depth and related climate conditions may support cedar dominance amid deciduous competitor species in areas characterized by mineral soils, sparse hummock microtopography, and moss cover.

Table 4 Unharvested and harvested plot characteristics by community type, with mean (± standard error)

Community characteristic	Unharvested Plots			Harvested Plots					
	Cedar- deciduous	Cedar- conifer	Cedar- shrub	Aspen-fir	Winterberry-willow	Balsam fir	Cedar-red maple	Cedar-black spruce	Alder- tamarack
Stand age (years)	NA	NA	NA	29.6 ± 1.9	29.8 ± 2.2	35.6 ± 0.8	33.3 ± 4.7	38.9 ± 1.9	32.6 ± 1.8
Soil pH	6.4 ± 0.1	6.6 ± 0.1	6.5 ± 0.1	6.61 ± 0.1	6.65 ± 0.1	6.78 ± 0.08	7.0 ± 0.23	6.61 ± 0.15	6.72 ± 0.09
Organic soils*	0.5 ± 0.1	0.7 ± 0.0	0.8 ± 0.1	0.7 ± 0.1	0.9 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.9 ± 0.1
Latitude (DD°)	45.9 ± 0.2	45.8 ± 0.1	45.9 ± 0.1	45.5 ± 0.1	45.7 ± 0.2	45.5 ± 0.1	45.9 ± 0.1	45.9 ± 0.1	45.7 ± 0.1
Snow depth (mm)	282.5 ± 14.6	247.6 ± 5.6	249.4 ± 12.9	215.7 ± 7.3	231.8 ± 6.4	238.6 ± 8.2	240.6 ± 14.2	248.9 ± 9.3	243.5 ± 7.9
Hummock (%)	12.8 ± 1.9	21.3 ± 1.5	25.2 ± 3.3	10.3 ± 1.5	16.5 ± 2.5	9.8 ± 1.6	18.0 ± 3.0	20.0 ± 2.3	13.4 ± 1.8
Pool (%)	17.0 ± 3.1	13.3 ± 1.1	18.1 ± 2.7	14.5 ± 2.2	13.2 ± 1.6	12.1 ± 2.0	17.3 ± 3.8	8.5 ± 1.8	14.8 ± 2.3
Moss (% cover)	20.0 ± 3.3	36.2 ± 2.4	42.4 ± 5.1	25.6 ± 3.1	17.1 ± 2.1	28.7 ± 3.2	25.3 ± 6.3	45.7 ± 4.8	23.9 ± 2.9
Canopy closure (%)	66.5 ± 3.3	68.7 ± 1.5	56.7 ± 3.5	50.3 ± 4.3	22.0 ± 6.2	70.7 ± 2.3	57.9 ± 6.2	42.3 ± 4.8	38.4 ± 4.1
CWM diameter (cm)	12.8 ± 0.8	12.9 ± 0.4	9.2 ± 0.9	12.39 ± 0.9	11.8 ± 1.1	12.2 ± 1.1	15.1 ± 1.6	12.3 ± 2.0	10.4 ± 1.4
White-cedar relative density	0.14 ± 0.04	0.24 ± 0.02	0.43 ± 0.05	0.13 ± 0.03	0.11 ± 0.03	0.13 ± 0.03	0.33 ± 0.06	0.38 ± 0.06	0.12 ± 0.03
White-cedar relative basal area	0.44 ± 0.06	0.79 ± 0.02	0.74 ± 0.04	0.23 ± 0.05	0.38 ± 0.11	0.16 ± 0.04	0.87 ± 0.04	0.41 ± 0.08	0.16 ± 0.05
White-cedar overstory D (cm)	25.7 ± 3.0	25.5 ± 0.6	19.4 ± 0.9	10.3 ± 1.8	8.8 ± 2.5	7.5 ± 1.7	26.7 ± 0.8	11.8 ± 2.1	5.4 ± 1.5
White-cedar seedling density (stems/ha)	3057.8 ± 716.4	6751.4 ± 975.5	17,002.9 ± 3557.0	4662.4 ± 1273.4	3722.4 ± 919.0	3411.5 ± 911.5	20,228.8 ± 7229.0	12,654.8 ± 4091.2	3553.2 ± 1,188.3
White-cedar sapling density (stems/ha)	383.4 ± 182.3	614.0 ± 105.5	2919.0 ± 585.4	269.2 ± 143.5	81.8 ± 60.6	1145.9 ± 297.5	657.3 ± 237.7	4880.5 ± 1153.5	729.0 ± 303.0

*Community characteristic was marked as present (value of 1) or absent (value of zero) within each plot

Table 5 White-cedar community type (based on Hierarchical Cluster Analysis) dominant species characteristics for 193 harvested plots. Basal area calculated for trees 15.2 cm D and larger; density calculated for all stem sizes

Community type ($n = 193$)	Dominant species	Common name	Basal area (m²/ha)	Density (stems/ha)
Aspen-fir ($n = 45$)	*Populus tremuloides* Michx.	Quaking aspen	1.31 ± 0.46	537.03 ± 198.06
	Populus balsamifera L.	Balsam poplar	1.01 ± 0.36	1102.07 ± 349.31
	Abies balsamea (L.) Mill	Balsam fir	0.69 ± 0.26	6182.92 ± 1291.42
	Betula alleghaniensis Britt.	Yellow birch	0.61 ± 0.38	942.52 ± 410
	Acer spicatum Lam.	Mountain maple	0 ± 0	1614.36 ± 732.72
Winterberry- willow ($n = 20$)	*Ilex verticillata* (L.) A. Gray	Winterberry	0 ± 0	8851.46 ± 2091.8
	Salix species	Willow	0 ± 0	3619.8 ± 992.17
	Betula papyrifera Marshall	Paper birch	0 ± 0	2747.84 ± 710.14
Balsam fir ($n = 41$)	*Abies balsamea* (L.) Mill	Balsam fir	0.24 ± 0.09	17,432.58 ± 1514.62
	Thuja occidentalis L.	White-cedar	1.26 ± 0.4	5828.93 ± 1373.6
Cedar-red maple ($n = 15$)	*Thuja occidentalis* L.	White-cedar	32.6 ± 4.84	22,782.7 ± 7397.03
	Acer rubrum L.	Red maple	1.06 ± 0.48	9360.98 ± 2209.94
	Fraxinus nigra Marshall	Black ash	0.28 ± 0.18	4746.08 ± 1584.79
Cedar-black spruce ($n = 32$)	*Picea mariana* (Mill.) Britton	Black spruce	1.54 ± 0.6	4173.44 ± 512.93
	Thuja occidentalis L.	White-cedar	6.03 ± 1.67	23,891.94 ± 5711.15
	Pinus strobus L.	White pine	0.41 ± 0.19	56.57 ± 36.12
	Larix laricina (Du Roi) K. Koch	Tamarack	0.31 ± 0.16	2172.79 ± 1123.22
Alder-tamarack ($n = 40$)	*Alnus incana* (L.) Moench	Grey alder	0 ± 0	13,521.79 ± 1538.04
	Larix laricina (Du Roi) K. Koch	Tamarack	0.95 ± 0.33	1594.37 ± 355.46
	Viburnum cassinoides L.	Wild raisin	0 ± 0	4357.47 ± 2552.35

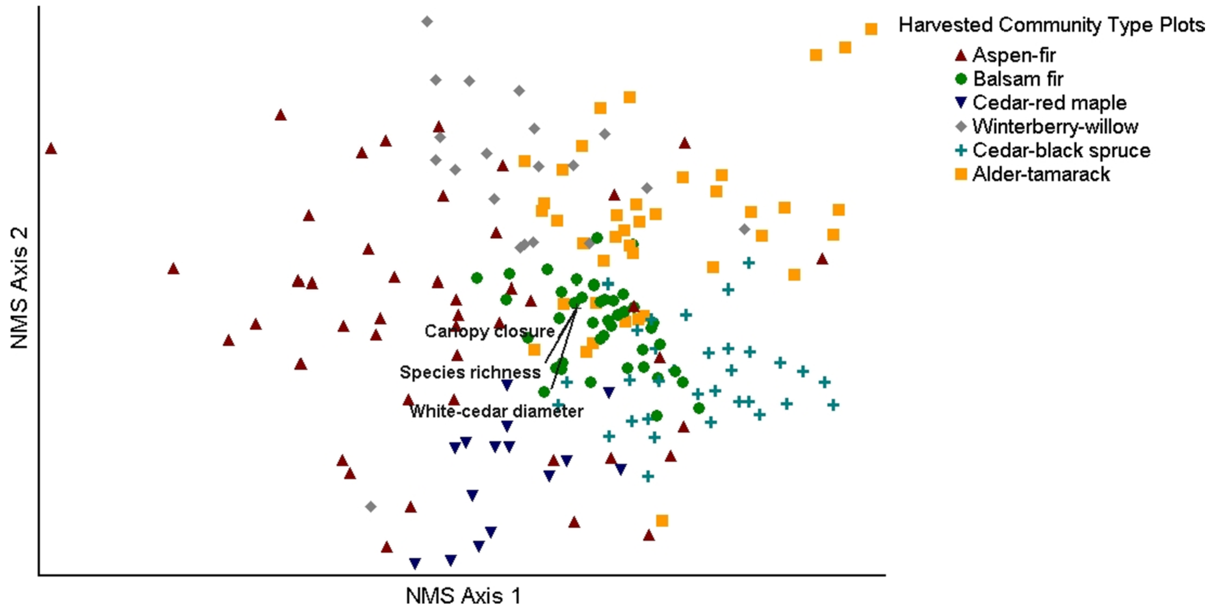

Fig. 4 Non-metric Multidimensional Scaling solution of six community types in harvested plots with ecological variables with r² values greater than 0.070 shown as vectors on axes 1 (28.2% of variance explained) and 2 (17.3% of variance explained), where vector length is proportional to explanatory strength (axis 3 not shown)

Table 6 Pearson (r^2) and Kendall ranked (tau) correlations of ecological variables with ordination axes for the NMS analysis of community types in harvested plots, with r^2 values greater than 0.070 on one or more axes

Variable	Axis 1		Axis 2		Axis 3	
	r^2	tau	r^2	tau	r^2	tau
White-cedar overstory D	0.061	–0.21	0.195	–0.338	0.041	–0.141
Species richness	0.076	–0.257	0.132	–0.207	0.008	–0.06
Canopy closure	0.044	–0.144	0.072	–0.165	0.003	0.002

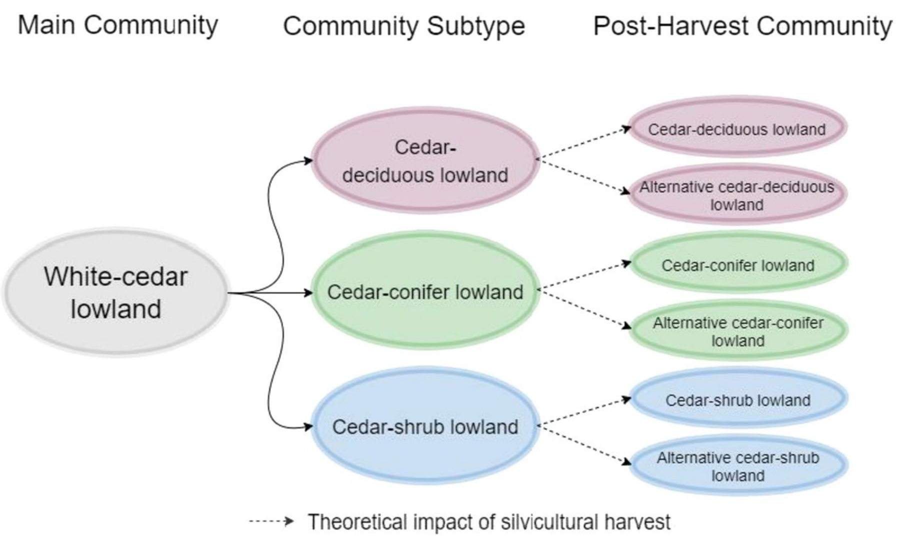

Fig. 5 Theoretical model of relationships among white-cedar community types in unharvested and harvested stands

The differences in soil pH among communities in unharvested and harvested stands was an interesting finding. Timber harvesting has been associated with soil acidification (Olsson et al. 1996), yet soil pH tended to be higher among harvested plots, compared with unharvested plots. Because pH is unlikely to increase through silvicultural treatment, we infer that sites with higher pH tend to be harvested more often than sites with lower pH. Taking this one step further, the sites with higher pH may better regenerate white-cedar while the sites with comparatively low pH may be prone to white-cedar replacement by alder, black spruce, and other associates.

Stand age and developmental stages also influenced the harvested plot community analysis. Two community types in harvested stands (aspen-fir and winterberry-willow) had lower mean stand ages than the four other community types (Table 4). These "younger" community types were dominated by faster growing, early successional white-cedar-associate species, within different environments characterized by both wetter, organic soils (winterberry-willow) and relatively drier, mineral soils (aspen-fir).

We hypothesize that white-cedar regeneration may be hindered differently in each community subtype. In the wet cedar-shrub community subtype, harvesting can make the site even wetter by removing trees and reducing evapotranspiration (Hubbart et al. 2007). Since white-cedars are limited by very wet conditions (Chimner and Hart 1996; Kangas et al. 2016) and alders, willows, and winterberry shrubs thrive in wet conditions, timber harvest in these sites is likely to favor these shrub species over white-cedar. In the cedar-deciduous community subtype, wetness is not the problem, but increased competition is. The cedar-deciduous community subtype occurs more often on wet mineral soils, which tend to be more nutrient rich than organic soils (Trettin et al. 2020). Timber harvesting opens up the canopy, allowing increased light and temperatures that fast-growing deciduous trees can take advantage of over the more slow-growing white-cedars. In addition, all three white-cedar community subtypes can experience white-cedar recruitment failures due to high browsing pressure from deer, pushing these communities toward non-cedar dominance (Cornett et al. 2000a; Heitzman et al.1997).

Caveats

This study sought to better understand lowland white-cedar community diversity, the potential effects of site conditions on white-cedar response to harvesting, and related potential trajectories in forest community composition. Because we did not have pre- and post-treatment data, we could not compare direct changes in forest community composition due to silvicultural treatments. The use of paired "parent" unharvested plots, selected in proximity to harvested plots, allowed us to assess harvest impacts with some confidence though neither pre-harvest data nor reports of the number, species, or size of harvested trees were available. Often, these plots were in the same stand or management unit, but fell within harvested and unharvested areas of strip or patch cuts, increasing the likelihood that they are representative. Further, though we use the term harvesting to describe the felling and removal of merchantable-sized trees broadly in this retrospective study, there was undoubtedly variation in the specifics of this practice among study sites. The intensity, spatial arrangement, and seasonal timing of harvests, for example, may vary with silvicultural prescription, landowner objectives, and operational constraints (Boulfroy et al. 2012). Whether this variation was related to attributes of the unharvested white-cedar community subtypes (e.g., commercial desirability of associate species) is unknown and likely to change with external and dynamic factors such as market availability. The diversity of stand ages in harvested plots (approximately 10 to 67 years) imply a range of successional and developmental stages among plots, which further contribute complexity to our analysis. Even with these complexities, the consistency in our findings across a broad range of silvicultural treatments, lapse times since harvest, and widespread geographic distribution suggests that conclusions are robust for a range of harvesting scenarios. Future work utilizing repeated measures and beginning before harvesting - ideally in designed experiments to minimize potential confounding factors - may validate the developmental pathways proposed here.

Management implications

Habitat classification integration with forest management brings basic information on stand development, composition, and site conditions into developing suitable treatments to perpetuate the type. Habitat classification of white-cedars vary from one to few types such that management guides for lowland white-cedar forests are broad. By treating lowland white-cedar stands (forested wetlands) as monolithic, resource managers have failed to discern the nuances associated with variation in species composition and site that influence response to harvesting disturbance. This study, along with previous research, supports the finding that timber harvest treatments are associated with declines in white-cedar. However, this study also found a minority of stands that maintained white-cedars or are on a trajectory to sustain the type into the future. Consequently, we suggest further research into more narrow than broad classifications to clarify management options.

The findings of the present study suggest that there are identifiable community subtypes associated with a range of pre-harvest lowland white-cedar stand compositions, and that these subtypes have the potential to influence response to harvesting. By identifying potential species transitions, practitioners can better determine which silvicultural treatments are likely to maintain white-cedar. Regardless of subtype, retaining seed sources for regeneration establishment and protecting and releasing advance regeneration of white-cedar are advisable (Boulfroy et al. 2012). Further subtype-specific adjustments may increase likelihood of achieving desired outcomes, e.g., retaining high residual stand stocking in the cedar-shrub community subtype to avoid increasing site wetness to the advantage of alder, or tending to control competition from rapid-growing and sprouting hardwoods or balsam fir after harvesting in cedar-deciduous and cedar-conifer community subtypes, respectively. Experimental and operational implementation of these treatments will help to inform their effectiveness.

Conclusion

Given past, present, and projected future changes, it is important to understand the diverse plant communities in which white-cedars grow, community types in harvested forests, and their relationships with ecological gradients on the landscape. The lowland white-cedar community types identified through this study provide a useful perspective with which to better understand the factors influencing white-cedar forest community dynamics and can be used in tailoring forest management strategies to specific community types and ecological gradients for improved outcomes.

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Author contributions Study conception and design for Phase I was led by RMC and RC. All authors contributed to Phase II study conception and design. Data collection was performed by RMC and field crews from Michigan Technological University. Material preparation and data analysis was performed by RMC. Writing of the first draft manuscript was performed by RMC and RC. All authors contributed to data interpretation, manuscript revisions, and have read and approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request. Data related to Phase I are available from the corresponding author on request and with approval of the Sault Ste. Marie Tribe of Chippewa Indians and Bay Mills Indian Community per Tribal-University Data Sharing Agreements.

Declarations

Competing interests The authors declare no competing interests.

Appendix

See Tables 7, 8, 9 and 10

Table 7 Plot-level ecological variables assessed in this study are included with short descriptions and mean ± standard error for unharvested and harvested plots

Variable	Description	Unharvested Plot Mean ± SE	Harvested Plot Mean ± SE
Basal area of balsam fir	Basal area of *Abies balsamea* stems > 15.2 cm D in m² per hectare	0.72 ± 0.13	0.29 ± 0.07
Basal area of balsam poplar	Basal area of *Populus balsamifera* stems > 15.2 cm D in m² per hectare	0.11 ± 0.05	0.26 ± 0.09
Basal area of black ash	Basal area of *Fraxinus nigra* stems > 15.2 cm D in m² per hectare	0.21 ± 0.07	0.04 ± 0.02
Basal area of black spruce	Basal area of *Picea mariana* stems > 15.2 cm D in m² per hectare	2.53 ± 0.3	0.57 ± 0.12
Basal area of white-cedar	Basal area of *Thuja occidentalis* stems > 15.2 cm D in m² per hectare	27.46 ± 1.38	4.78 ± 0.78
Basal area of paper birch	Basal area of *Betula papyrifera* stems > 15.2 cm D in m² per hectare	0.87 ± 0.13	0.17 ± 0.03
Basal area of quaking aspen	Basal area of *Populus tremuloides* stems > 15.2 cm D in m² per hectare	0.32 ± 0.14	0.36 ± 0.12
Basal area of red maple	Basal area of *Acer rubrum* stems > 15.2 cm D in m² per hectare	1.18 ± 0.22	0.22 ± 0.06
Basal area of sugar maple	Basal area of *Acer saccharum* stems > 15.2 cm D in m² per hectare	0.05 ± 0.03	0 ± 0
Basal area of tamarack	Basal area of *Larix laricina* stems > 15.2 cm D in m² per hectare	0.51 ± 0.12	0.38 ± 0.09
Basal area of yellow birch	Basal area of *Betula alleghaniensis* stems > 15.2 cm D in m² per hectare	0.54 ± 0.15	0.16 ± 0.09
Basal area of white pine	Basal area of *Pinus strobus* stems > 15.2 cm D in m² per hectare	0.87 ± 0.24	0.19 ± 0.05
Basal area of white spruce	Basal area of *Picea glauca* stems > 15.2 cm D in m² per hectare	0.18 ± 0.08	0.08 ± 0.04
Canopy closure	Average percent of area covered by tree canopy	65.93 ± 1.33	48.52 ± 2.06
Cedar quadratic mean diameter	Quadratic mean diameter (cm) of *Thuja occidentalis* stems > 15.2 cm D	24.32 ± 0.67	10.05 ± 0.86
Cedar seedling density	Number of *Thuja occidentalis* stems > 1 m height per hectare	8190.56 ± 1004.18	6604.35 ± 1035.8
Cedar sapling density	Number of *Thuja occidentalis* stems ≥ 0.3 m height and < 12.7 cm D per hectare	1038.62 ± 154.21	1326.06 ± 241.99
Coarse woody material decay class	Mean decay class of coarse woody material (> 2.5 cm)	3.44 ± 0.08	3.29 ± 0.12

Table 7 (continued)

Variable	Description	Unharvested Plot Mean ± SE	Harvested Plot Mean ± SE
Coarse woody material diameter	Mean diameter of coarse woody material (> 2.5 cm)	11.62 ± 0.35	12.04 ± 0.56
Density of grey alder	Number of *Alnus incana* stems per hectare	3363.65 ± 571.52	6329.34 ± 600.11
Density of balsam fir	Number of *Abies balsamea* stems per hectare	10440.22 ± 1121.78	8533.96 ± 727.41
Density of balsam poplar	Number of *Populus balsamifera* stems per hectare	43.04 ± 17.52	459.2 ± 106.43
Density of black ash	Number of *Fraxinus nigra* stems per hectare	1890.23 ± 439.39	1338.84 ± 291.38
Density of black spruce	Number of *Picea mariana* stems per hectare	1467.8 ± 212.16	1411.77 ± 148.2
Density of white-cedar	Number of *Thuja occidentalis* stems per hectare	12,585 ± 1532.39	10,049.08 ± 1360.87
Density of glossy buckthorn	Number of *Rhamnus frangula* stems per hectare	0 ± 0	132.79 ± 47.15
Density of mountain maple	Number of *Acer spicatum* stems per hectare	922.74 ± 506.26	465.65 ± 179.46
Density of paper birch	Number of *Betula papyrifera* stems per hectare	332.82 ± 98.97	1168.1 ± 175.75
Density of quaking aspen	Number of *Populus tremuloides* stems per hectare	71.12 ± 35.98	343.86 ± 86.43
Density of red maple	Number of *Acer rubrum* stems per hectare	10,618.82 ± 1221.8	5276.47 ± 623.54
Density of sugar maple	Number of *Acer saccharum* stems per hectare	711.32 ± 197.41	125.83 ± 63.61
Density of tamarack	Number of *Larix laricina* stems per hectare	403.07 ± 134.02	789.9 ± 208.32
Density of white pine	Number of *Pinus strobus* stems per hectare	154.98 ± 71.01	52.55 ± 17.96
Density of white spruce	Number of *Picea glauca* stems per hectare	86.6 ± 34.01	23.02 ± 11.91
Density of wild raisin	Number of *Viburnum cassinoides* stems per hectare	132.05 ± 70.18	1209.65 ± 544.26
Density of willow	Number of *Salix* stems per hectare	165.31 ± 86.36	1339.26 ± 245.25
Density of winterberry	Number of *Illex verticillata* stems per hectare	919.3 ± 283.25	1443.38 ± 315.67
Density of yellow birch	Number of *Betula allegheniensis* stems per hectare	251.71 ± 80.82	258.24 ± 101.75
Hummock microtopography	Percent of microtopography as hummock (areas raised 0.3 m or greater than surrounding area)	20.67 ± 1.21	13.68 ± 0.84
Latitude	Geographic coordinate of plot center as decimal degrees north	45.83 ± 0.05	45.65 ± 0.05
Longitude	Geographic coordinate of plot center as decimal degrees west	− 85.44 ± 0.09	85.55 ± 0.09
Moss cover	Percent of bryophyte cover recorded as the center point of one of 5 classes: 0%, 1– 25%, 26–50%, 51–75%, and 76–100%	34.73 ± 1.98	28.34 ± 1.6

Table 7 (continued)

Variable	Description	Unharvested Plot Mean ± SE	Harvested Plot Mean ± SE
Organic soil	Proportion of plots with soil dominated by organic material at least 40 cm below soil surface (if not, mineral soil)	0.7 ± 0.03	0.77 ± 0.03
Pool microtopography	Percent of microtopography as pool (areas saturated with water during all or part of the growing season)	14.85 ± 1.04	13.14 ± 0.94
Relative basal area of balsam fir	Proportion of total basal area composed of *Abies balsamea* stems > 15.2 cm D	0.03 ± 0	0.04 ± 0.01
Relative basal area of black spruce	Proportion of total basal area composed of *Picea mariana* stems > 15.2 cm D	0.08 ± 0.01	0.11 ± 0.02
Relative basal area of white-cedar	Proportion of total basal area composed of *Thuja occidentalis* stems > 15.2 cm D	0.72 ± 0.02	0.3 ± 0.03
Relative basal area of paper birch	Proportion of total basal area composed of *Betula papyrifera* stems > 15.2 cm D	0.03 ± 0	0.03 ± 0.01
Relative basal area of red maple	Proportion of total basal area composed of *Acer rubrum* stems > 15.2 cm D	0.04 ± 0.01	0.03 ± 0.01
Relative basal area of tamarack	Proportion of total basal area composed of *Larix laricina* stems > 15.2 cm D	0.03 ± 0.01	0.09 ± 0.02
Relative basal area of yellow birch	Proportion of total basal area composed of *Betula allegheniensis* stems > 15.2 cm D	0.02 ± 0.01	0.01 ± 0.01
Relative density of balsam fir	Proportion of total stems > 15.2 cm D composed of *Abies balsamea*	0.04 ± 0.01	0.05 ± 0.01
Relative density of black spruce	Proportion of total stems > 15.2 cm D composed of *Picea maraiana*	0.1 ± 0.01	0.12 ± 0.02
Relative density of white-cedar	Proportion of total stems > 15.2 cm D composed of *Thuja occidentalis*	0.69 ± 0.02	0.28 ± 0.03
Relative density of paper birch	Proportion of total stems > 15.2 cm D composed of *Betula papyrifera*	0.03 ± 0	0.03 ± 0.01
Relative density of quaking aspen	Proportion of total stems > 15.2 cm D composed of *Populus tremuloides*	0.01 ± 0	0.03 ± 0.01
Relative density of red maple	Proportion of total stems > 15.2 cm D composed of *Acer rubrum*	0.04 ± 0.01	0.03 ± 0.01
Relative density of tamarack	Proportion of total stems > 15.2 cm D composed of *Larix laricena*	0.03 ± 0.01	0.09 ± 0.02
Relative density of yellow birch	Proportion of total stems > 15.2 cm D composed of *Abies balsamea*	0.02 ± 0	0.01 ± 0.01
Snow depth	Mean annual snow depth in millimeters (October-March 2003 to 2019)	253.83 ± 5.09	235.44 ± 3.62
Soil pH	Soil water pH measured at soil surface or up to 10 cm below the soil surface	6.56 ± 0.06	6.7 ± 0.05

Table 7 (continued)

Variable	Description	Unharvested Plot Mean ± SE	Harvested Plot Mean ± SE
Stand age	Number of years since documented timber harvest	NA	33.35 ± 0.83

Variables for which mean values are significantly different across unharvested and harvested plots are indicated with an asterisk

Table 8 Pearson and Kendall Correlations for Unharvested Plots

	Axis 1		Axis 2		Axis 3	
	r^2	tau	r^2	tau	r^2	tau
Total basal area (all species)	0.629	− 0.614	0.082	− 0.218	0.04	0.143
White-cedar quadratic mean diameter	0.247	− 0.411	0.047	− 0.066	0.035	− 0.024
White-cedar sapling density	0.189	0.26	0.003	−0.057	0.071	− 0.144
Coarse woody material diameter	0.122	− 0.199	0.001	0.001	0.003	− 0.044
Canopy closure	0.094	− 0.187	0.002	0.026	0.021	0.151
Moss cover	0.053	0.195	0.068	− 0.21	0.006	0.062
Coarse woody material decay class	0.052	− 0.092	0.001	0.011	0.002	0
White-cedar seedling density	0.051	0.109	0.045	− 0.207	0.032	− 0.135
Pool microtopography	0.033	0.114	0.014	0.051	0.042	− 0.096
Hummock microtopography	0.028	0.1	0.046	− 0.122	0	− 0.015
Latitude	0.02	0.091	0.004	0.031	0.007	− 0.151
Soil pH	0.014	− 0.048	0.09	− 0.171	0.004	− 0.04
Species richness	0.059	− 0.116	0.051	− 0.183	0.062	0.171
Snow depth	0.007	0.028	0.026	0.033	0.018	− 0.101
Organic soils	0.003	0.036	0.125	− 0.264	0.006	− 0.058

Table 9 Pearson and Kendall Correlations for Harvested Plots

	Axis 1		Axis 2		Axis 3	
	r^2	tau	r^2	tau	r^2	tau
White-cedar quadratic mean diameter	0.061	− 0.21	0.195	− 0.338	0.041	− 0.141
Species richness	0.076	− 0.257	0.132	− 0.207	0.008	− 0.06
Canopy closure	0.044	− 0.144	0.072	− 0.165	0.003	0.002
Snow depth	0.065	0.135	0.01	− 0.038	0.007	0.07
White-cedar sapling density	0.058	0.149	0.015	− 0.207	0.041	− 0.166
Coarse woody material decay class	0.057	− 0.088	0.008	− 0.029	0.003	0.047
Moss cover	0.045	0.163	0.041	− 0.144	0.035	− 0.123
Coarse woody material diameter	0.029	− 0.131	0.014	− 0.06	0	0.001
Hummock microtopography	0.026	0.118	0.01	− 0.061	0.002	− 0.028
Latitude	0.023	0.125	0.021	− 0.108	0.005	0.043
Stand age	0.016	0.13	0.041	− 0.15	0.005	0.046
Organic soils	0.014	0.093	0.002	0.022	0.001	0.035
Soil pH	0.003	− 0.019	0.004	− 0.048	0.004	− 0.06
White-cedar seedling density	0.001	− 0.088	0.028	− 0.012	0.026	− 0.227
Pool microtopography	0	− 0.045	0.002	0.078	0.011	0.075

Table 10 Values for all community type characteristics considered in the study

Variable	Cedar– deciduous	Cedar– conifer	Cedar- shrub	Aspen-fir	Winterberry- willow	Balsam fir	Cedar-red maple	Cedar-black spruce	Alder- tamarack
Stand age	120.13 ± 0.18	120.49 ± 0.07	120.22 ± 0.15	29.64 ± 1.89	29.8 ± 2.23	35.56 ± 0.83	33.27 ± 4.69	38.94 ± 1.86	32.6 ± 1.83
Basal area of balsam fir	2.42 ± 0.62	0.46 ± 0.07	0.14 ± 0.08	0.69 ± 0.26	0 ± 0	0.24 ± 0.09	0.26 ± 0.23	0.05 ± 0.04	0.24 ± 0.14
Basal area of red maple	4.82 ± 0.96	0.51 ± 0.12	0.21 ± 0.11	0.3 ± 0.18	0.15 ± 0.11	0.18 ± 0.12	1.06 ± 0.48	0.01 ± 0.01	0.04 ± 0.03
Basal area of sugar maple	0.24 ± 0.17	0.01 ± 0.01	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Basal area of yellow birch	2.46 ± 0.76	0.2 ± 0.08	0 ± 0	0.61 ± 0.38	0 ± 0	0 ± 0	0.18 ± 0.18	0 ± 0	0 ± 0
Basal area of paper birch	0.65 ± 0.23	1.17 ± 0.18	0.1 ± 0.04	0.26 ± 0.1	0 ± 0	0.13 ± 0.07	0.51 ± 0.15	0.12 ± 0.08	0.1 ± 0.04
Basal area of black ash	0.22 ± 0.1	0.27 ± 0.11	0 ± 0	0.07 ± 0.04	0 ± 0	0.02 ± 0.02	0.28 ± 0.18	0 ± 0	0 ± 0
Basal area of tamarack	0 ± 0	0.11 ± 0.05	2.21 ± 0.48	0.12 ± 0.09	0 ± 0	0.48 ± 0.16	0 ± 0	0.31 ± 0.16	0.95 ± 0.33
Basal area of white spruce	0.98 ± 0.45	0.03 ± 0.02	0 ± 0	0.29 ± 0.17	0 ± 0	0 ± 0	0.14 ± 0.14	0 ± 0	0 ± 0
Basal area of black spruce	0.78 ± 0.38	3.44 ± 0.44	1.12 ± 0.33	0.14 ± 0.06	0 ± 0	0.88 ± 0.19	0.19 ± 0.11	1.54 ± 0.6	0.41 ± 0.14
Basal area of white pine	2.68 ± 1.17	0.62 ± 0.2	0.14 ± 0.11	0.13 ± 0.1	0 ± 0	0.35 ± 0.11	0.18 ± 0.18	0.41 ± 0.19	0.03 ± 0.02
Basal area of balsam poplar	0 ± 0	0.16 ± 0.08	0.02 ± 0.02	1.01 ± 0.36	0 ± 0	0.04 ± 0.03	0 ± 0	0.02 ± 0.02	0.03 ± 0.03
Basal area of quaking aspen	1.66 ± 0.78	0.06 ± 0.03	0 ± 0	1.31 ± 0.46	0 ± 0	0.25 ± 0.12	0 ± 0	0 ± 0	0 ± 0
Basal area of white-cedar	18.77 ± 3	34.25 ± 1.59	13.45 ± 2.24	2.61 ± 0.8	1.55 ± 0.72	1.26 ± 0.4	32.6 ± 4.84	6.03 ± 1.67	1.04 ± 0.43
Basal area of elm	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.02 ± 0.02	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Density of balsam fir	5965.24 ± 1585.33	11401.66 ± 1134.71	11175.26 ± 4074.29	6182.92 ± 1291.42	2089.63 ± 705.04	17432.58 ± 1514.62	6175.36 ± 1554.18	9405.38 ± 1907.5	5467.29 ± 1482.2
Density of red maple	24054.97 ± 5039.46	8537.58 ± 1069.17	5886.47 ± 1831.97	6887.36 ± 1133.27	2969.7 ± 629.39	6986.89 ± 2188.66	9360.98 ± 2209.94	4500.46 ± 1247.71	1953.54 ± 387.14
Density of sugar maple	1848.71 ± 643.21	634.25 ± 255.07	0 ± 0	489.55 ± 263.16	0 ± 0	0 ± 0	0 ± 0	0 ± 0	56.4 ± 56.4

Table 10 (continued)

Variable	Cedar– deciduous	Cedar– conifer	Cedar- shrub	Aspen-fir	Winterberry- willow	Balsam fir	Cedar-red maple	Cedar-black spruce	Alder- tamarack
Density of mountain maple	4011.62 ± 2891.8	391.59 ± 192.25	0 ± 0	1614.36 ± 732.72	0 ± 0	115 ± 66.91	157.17 ± 150.07	35.25 ± 35.25	225.6 ± 157.46
Density of grey alder	2277.92 ± 1096.52	1836.63 ± 387.8	9060.73 ± 2186.17	3715.44 ± 913.2	7417.76 ± 1944.12	6240.68 ± 1295.99	2080.8 ± 660.32	2439.39 ± 755.05	13521.79 ± 1538.04
Density of yellow birch	966.83 ± 403.85	140.89 ± 60.39	0 ± 0	942.52 ± 410	0 ± 0	0 ± 0	249.23 ± 224.6	0 ± 0	92.21 ± 87.16
Density of paper birch	14.73 ± 5.76	425.91 ± 152	307.49 ± 114.36	929.92 ± 275.53	2747.84 ± 710.14	1299.07 ± 296.14	2109.72 ± 1486.84	439.1 ± 126.65	742.03 ± 237.37
Density of black ash	2322.72 ± 805.8	2360.99 ± 655.88	51.99 ± 36.82	2584.85 ± 965.84	2017.44 ± 649.4	547.55 ± 338.6	4746.08 ± 1584.79	0 ± 0	202.2 ± 150.66
Density of winterberry	226.8 ± 168.15	753.22 ± 256.01	2020.2 ± 1142.29	733.2 ± 358.06	8851.46 ± 2091.8	34.94 ± 27.87	526.4 ± 394.86	671.87 ± 459.85	943.01 ± 430.28
Density of tamarack	152.1 ± 113.82	157.34 ± 69.46	1383.73 ± 602.71	124.2 ± 51.69	424.14 ± 183.6	86.36 ± 42.3	102.27 ± 78.08	2172.79 ± 1123.22	1594.37 ± 355.46
Density of white spruce	339.69 ± 175.02	46.58 ± 24.52	0 ± 0	95.34 ± 49.93	0 ± 0	0 ± 0	3.32 ± 3.32	0 ± 0	2.54 ± 2.54
Density of black spruce	933.71 ± 568.4	1431.48 ± 243.75	2029.14 ± 549.32	787.27 ± 227.89	296.67 ± 151.14	1243.58 ± 191.17	1024.11 ± 372.81	4173.44 ± 512.93	780.32 ± 172.38
Density of white pine	43.04 ± 37.91	185.28 ± 101.35	153.78 ± 152.4	85.89 ± 46.48	56.4 ± 56.4	69.7 ± 54.89	1.66 ± 1.66	56.57 ± 36.12	11.4 ± 6.35
Density of balsam poplar	36.39 ± 36.39	48.6 ± 24.27	31.16 ± 30.48	1102.07 ± 349.31	204.73 ± 91.7	158.92 ± 109.85	150.4 ± 150.4	74.1 ± 45.35	594.86 ± 274.9
Density of quaking aspen	231.04 ± 151.07	51.07 ± 40.01	0 ± 0	537.03 ± 198.06	1524.53 ± 582.42	230.81 ± 135.01	0 ± 0	9.52 ± 9.52	48.51 ± 29.12
Density of glossy buckthorn	0 ± 0	0 ± 0	0 ± 0	25.07 ± 25.07	922.7 ± 343.5	0 ± 0	382.77 ± 311.37	0 ± 0	7.61 ± 7.61
Density of willow	0 ± 0	205.86 ± 133.76	176.68 ± 92.5	987.63 ± 392.78	3619.8 ± 992.17	257.36 ± 106.78	361.71 ± 305.75	226.66 ± 92.41	2960.17 ± 871.88
Density of white-cedar	4477.97 ± 1086.96	9619.93 ± 1365.79	28673.25 ± 5510.86	5784.72 ± 1494.55	4582.25 ± 1046.71	5828.93 ± 1373.6	22782.7 ± 7397.03	23891.94 ± 5711.15	6056.14 ± 1877.43
Density of elm	0.8 ± 0.8	9.94 ± 9.94	0 ± 0	91.55 ± 56.94	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Density of wild raisin	0 ± 0	199.73 ± 110.59	30.49 ± 30.49	601.6 ± 260.01	0 ± 0	525.21 ± 286.94	225.6 ± 163.28	224.19 ± 181.16	4357.47 ± 2552.35

Table 10 (continued)

Variable	Cedar– deciduous	Cedar– conifer	Cedar- shrub	Aspen-fir	Winterberry- willow	Balsam fir	Cedar-red maple	Cedar-black spruce	Alder- tamarack
Canopy closure	66.5 ± 3.3	68.74 ± 1.48	56.65 ± 3.49	50.33 ± 4.25	22.03 ± 6.22	70.74 ± 2.29	57.88 ± 6.18	42.26 ± 4.83	38.43 ± 4.1
CWM decay class	3.5 ± 0.12	3.56 ± 0.09	3.02 ± 0.24	3.44 ± 0.2	3.35 ± 0.29	3.46 ± 0.27	3.8 ± 0.26	3.31 ± 0.32	2.7 ± 0.32
CWM diameter	12.78 ± 0.76	12.08 ± 0.41	9.19 ± 0.86	12.31 ± 0.87	11.78 ± 1.11	12.17 ± 1.11	15.14 ± 1.59	12.27 ± 1.96	10.41 ± 1.37
Hummock micro.	12.79 ± 1.91	21.34 ± 1.46	25.18 ± 3.3	10.32 ± 1.53	16.52 ± 2.5	9.79 ± 1.61	18.03 ± 3.02	19.98 ± 2.33	13.35 ± 1.76
Latitude	45.92 ± 0.16	45.8 ± 0.06	45.87 ± 0.11	45.48 ± 0.12	45.71 ± 0.15	45.45 ± 0.08	45.9 ± 0.13	45.89 ± 0.09	45.69 ± 0.1
Longitude	− 85.7 ± 0.23	− 85.5 ± 0.12	− 85.03 ± 0.19	− 85.49 ± 0.2	− 86.48 ± 0.25	− 84.74 ± 0.1	− 85.9 ± 0.35	− 85.47 ± 0.19	− 85.89 ± 0.19
Moss cover	19.98 ± 3.25	36.22 ± 2.41	42.39 ± 5.11	25.62 ± 3.08	17.1 ± 2.08	28.68 ± 3.18	25.33 ± 6.26	45.72 ± 4.84	23.9 ± 2.85
White-cedar saplings/ha	383.38 ± 182.31	613.96 ± 105.45	2918.99 ± 585.39	269.23 ± 143.52	81.78 ± 60.62	1145.93 ± 297.52	657.28 ± 237.66	4880.5 ± 1153.45	728.99 ± 302.97
White-cedar seedling/ha	3057.8 ± 716.35	6751.42 ± 975.48	17002.89 ± 3556.97	4662.4 ± 1273.36	3722.4 ± 918.95	3411.51 ± 911.54	20228.8 ± 7228.98	12654.75 ± 4091.19	3553.2 ± 1188.25
Soil pH	6.35 ± 0.14	6.63 ± 0.07	6.52 ± 0.13	6.61 ± 0.1	6.65 ± 0.1	6.78 ± 0.08	7 ± 0.23	6.61 ± 0.15	6.72 ± 0.09
Pool micro.	17.02 ± 3.08	13.25 ± 1.12	18.06 ± 2.73	14.51 ± 2.16	13.15 ± 1.6	12.13 ± 2.04	17.27 ± 3.83	8.53 ± 1.82	14.78 ± 2.31
Mean diameter overstory white-cedar	25.67 ± 2.96	25.53 ± 0.58	19.43 ± 0.91	10.26 ± 1.85	8.8 ± 2.49	7.5 ± 1.72	26.71 ± 0.81	11.78 ± 2.06	5.42 ± 1.54
Relative BA white-cedar	0.44 ± 0.06	0.79 ± 0.02	0.74 ± 0.04	0.23 ± 0.05	0.38 ± 0.11	0.16 ± 0.04	0.87 ± 0.04	0.41 ± 0.08	0.16 ± 0.05
Annual snow depth	282.54 ± 14.61	247.59 ± 5.62	249.35 ± 12.94	215.66 ± 7.28	231.83 ± 6.35	238.64 ± 8.21	240.58 ± 14.15	248.89 ± 9.34	243.51 ± 7.95
Organic soil	0.45 ± 0.09	0.72 ± 0.04	0.81 ± 0.06	0.67 ± 0.07	0.85 ± 0.08	0.78 ± 0.06	0.67 ± 0.13	0.78 ± 0.07	0.85 ± 0.06
Relative density white-cedar overstory	0.14 ± 0.04	0.24 ± 0.02	0.43 ± 0.05	0.13 ± 0.03	0.11 ± 0.03	0.13 ± 0.03	0.33 ± 0.06	0.38 ± 0.06	0.12 ± 0.03

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