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# Structural and Spatial Characteristics of Old-Growth Temperate Deciduous Forests at Their Northern Distribution Limit

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Relic old-growth forests are unique witnesses of long-term forest dynamics that can be used as reference conditions for ecosystem-based forest management. In temperate deciduous forests, catastrophic stand-replacing disturbances are rare, and stand dynamics are controlled by endogenous tree-by-tree replacement. Processes might be different at the northern distribution limit of temperate deciduous forests, because of differences in climate and disturbance regimes. We studied tree species composition, diameter, age, and spatial structures of 11 old-growth temperate deciduous stands across an age gradient. Stand characteristics differed from expectation, based on previous studies that were conducted in the central region of the range of temperate deciduous forests. Instead of increasing with age, tree species richness was higher in stands $<120$ years old because of the presence of relatively short-lived species such as *Abies balsamea* and *Acer rubrum.* All diameter distributions followed a two- or three-parameter Weibull model, instead of a rotated sigmoid. Some age structures showed recruitment pulses, contrary to the expectation of constant recruitment, and the spatial distribution of living trees was mostly random with regard to age and species at assessed distances ($<14$ m). In the context of ecosystem-based forest management, our results suggest that harvest levels should vary across harvesting blocks and selection silviculture should occasionally include larger, multiple-tree gaps in addition to single-tree gaps.

**Keywords:** spatial structure, size distribution, age structure, northern limit, sugar maple, *Acer saccharum*, yellow birch, *Betula alleghaniensis*

Relic old-growth forests are unique witnesses of long-term forest dynamics and can serve to establish ecological boundaries that support ecosystem-based forest management (Landres et al. 1999, Gauthier et al. 2009). This is particularly important in temperate deciduous forests, where catastrophic disturbances are rare, allowing endogenous tree-by-tree replacement to dominate stand dynamics (Payette et al. 1990, Fraver et al. 2009). Under such a regime, old-growth stands develop uneven-aged structures that usually result in a rotated sigmoid distribution at equilibrium (Goff and West 1975, Lorimer et al. 2001, Rubin et al. 2006). However, old-growth temperate forests are complex, and their size or age distributions occasionally do not follow this distribution (Burrascano et al. 2013). Indeed, infrequent intermediate disturbances can interact with recurrent small-scale, low-intensity gap disturbances (Woods 2004, Hanson and Lorimer 2007). Such highly dynamic, small-scale shifting mosaic systems (Bormann and Likens 1979) result in varied local disturbance histories and residual structural patterns that generate heterogeneous growth conditions, which have important consequences for tree size and age structures (Canham et al. 1990, Beaudet and Messier 1998, Beaudet et al. 2000, Koukoulas and Blackburn 2005, Messier et al. 2009). Fine-scale spatial heterogeneity and tree-level processes can have major effects on forest-level properties (Pacala and Deutschman 1995). Therefore, understanding the complex spatial organization of trees could significantly improve our understanding of forest dynamics by identifying levels and scales of influence of stand development processes (Pommerening 2002, Pommerening and Särkkä 2013).

Although the structure and spatial organization of old-growth temperate deciduous forests have been well documented in the central part of their distribution range (Busing and White 1997, Burrascano et al. 2013, Runkle 2013), only one study has been conducted at their northern distribution limit (Payette et al. 1990). The dynamics of old-growth temperate deciduous forests could vary across their distribution range because of differences in climate conditions, disturbance regimes, and tree growth (Runkle 1982). For example, Payette et al. (1990) observed smaller gap sizes and faster

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canopy turnover at the northern distribution limit of temperate deciduous forests in Quebec (Canada). Such a pattern could be attributed to less suitable growth conditions that reduce longevity, limit crown development, and cause progressive limb shedding. Moreover, in the temperate deciduous forests of the northeastern United States, intermediate disturbances (Woods 2004) and large-scale catastrophic disturbances are more frequent under the influence of the North Atlantic hurricane zone (Frelich and Graumlich 1994). In addition to cooler climatic conditions, a different disturbance regime could subsequently lead to a different forest structure or spatial organization at the northern range limit of temperate deciduous forests.

Our objective was to describe tree species composition, age, size, and spatial structures of old-growth temperate deciduous forests at their northern distribution limit. Characterizing the structure of old-growth forests provides important information for forest managers (D'Amato and Orwig 2008, Silver et al. 2013). Recognizing and describing distinctive patterns in old-growth temperate deciduous forests at their northern distribution limit, when these are compared with more central locations within their range would help forest managers adapt ecosystem-based practices accordingly. Following studies that were conducted in the central region of the temperate deciduous forests, we hypothesized that (1) old-growth stands would be increasingly heterospecific with age, as new tree species are recruited through the stochastic process of gap dynamics (Hubbell 2001), (2) age structure would be monotonic as a result of continuous recruitment (Fraver et al. 2009), (3) diameter distribution would first follow a negative exponential or Weibull function indicating continuous recruitment (Rubin et al. 2006), before switching to a rotated sigmoid in the oldest stands, thereby indicating a low mortality rate for mature trees (Lorimer et al. 2001, Westphal et al. 2006), and (4) tree age and diameter would be randomly distributed regardless of stand age as a result of stochastic gap dynamics (Payette et al. 1990).

## Materials and Methods

### Study Area

The study sites were located within or slightly north of the sugar maple-yellow birch bioclimatic domain in western Quebec, Canada (46°70′–47°22′ N and 78°49′–78°89′ W) (Figure 1). This region covers 65,500 km$^2$ and is characterized by humo-ferric podzols (Brown 1981). The most abundant forest community in the area is sugar maple-yellow birch (*Betula alleghaniensis* Britton), with fewer occurrences of yellow birch-balsam fir (*Abies balsamea* [L.] Mill.), yellow birch-hemlock (*Tsuga canadensis* [L.] Carr.), and balsam fir-eastern white cedar (*Thuja occidentalis* L.) communities (Brown 1981). The climate is continental with cold winters and warm summers. Mean annual temperature is 4.4° C and total annual precipitation is 963 mm with an average of 23% falling as snow (Robitaille and Saucier 1998).

Frequent canopy openings created by the death of one or a few trees constitute the principal natural disturbance in the study area (Doyon and Sougavinski 2002). The fire cycle was estimated to be between 188 and 493 years, with the last major fire in the region occurring in 1923 AD (Grenier et al. 2005). Less than 5,000 ha of forests have burned since 1950 (Grenier et al. 2005, Drever et al. 2006, Roy et al. 2010). Catastrophic windthrows are less frequent than fire; their cycle were estimated to be between 1,700 and 7,000 years (Roy et al. 2010, Bégin 2011). However, a catastrophic windthrow had affected >25,000 ha of the study area in 2006 AD, with 30–100% of the forest canopy cover affected (Roy et al. 2010).

### Field Sampling

We sampled 11 old-growth forest stands, all of which were separated by at least 500 m (Figure 1). Old-growth stands are rare in the study area, where industrial forest management has been active for more than 70 years. Thus, sampled stands were located in protected areas (four in the Lake-Malakisis Ecological Reserve and four in Exceptional Forest Ecosystems) or on islands (three) (Figure 1). Island and mainland sites had similar disturbance rates (1.1 ± 0.55 and 1.3 ± 0.54% per year, respectively) (Tiphaine Després, Université du Québec en Abitibi-Témiscamingue, unpubl. data, July 8, 2013). Stand selection was based on three criteria: no trace of harvesting (i.e., every log could be associated with its stump); the presence of dead trees at different decomposition stages; and trees of different sizes.

In each stand, a 2,500-m$^2$ circular sample plot was randomly located, while making sure that a 100-m buffer zone was maintained between plots and roads, lakes, or other nonforested areas. All sampled stands were at least 5 ha in size. In each plot, we recorded the species of each individual, together with its dbh (1.3 m), height (social rank using Kraft classes; Schütz 1990), and crown area (approximated using the longest vertical projection of the branches and crown form: full circle, half circle, or quarter). The spatial location of every dead snag or living tree (dbh ≥ 9.1 cm) was registered using an ultrasonic rangefinder (Vertex IV Hypsometer, Haglöf, Inc., Madison, MS). For dead snags without a dbh, stump diameter was measured at 30 cm. We cored every living tree as close as possible to its base (usually within 20–30 cm above the ground surface), trying to reach the pith (three trials). We dried and sanded all cores.

### Dendrochronological Analysis

The cores were cross-dated using pointer years (Yamaguchi 1991). Cross-dating was statistically verified using COFECHA (Holmes 1983) (Table 1). A number of the resulting chronologies exhibited low average correlations when examined with COFECHA, but this was to be expected due to the large variation in local light conditions affecting the growth of shade-tolerant species. A pith locator was used to estimate pith position when the pith was not included in the core (Applequist 1958). We estimated the precision of the pith locator to be around 10–20 years because of tree-to-tree variability in growth patterns. Because of the poor age estimates with the pith locator, we considered all ages as being minimum estimates. Trees with heartrot could not be aged and, thus, were excluded from stand age calculation.

To assess the effect of stand age on forest community patterns, we used the 90th percentile for the age distribution of trees, which had been successfully aged. This age indicator was used to rank forest communities according to the minimum time since the last stand-replacing disturbance. This approach is similar to that proposed by Keeton et al. (2007, 2011), who used the oldest cohort of trees as an index of stand age.

### Stand Structure

We calculated an importance value (Curtis and McIntosh 1951) as the average of relative density and relative dominance (basal area) to characterize the species composition in each plot. We fitted the

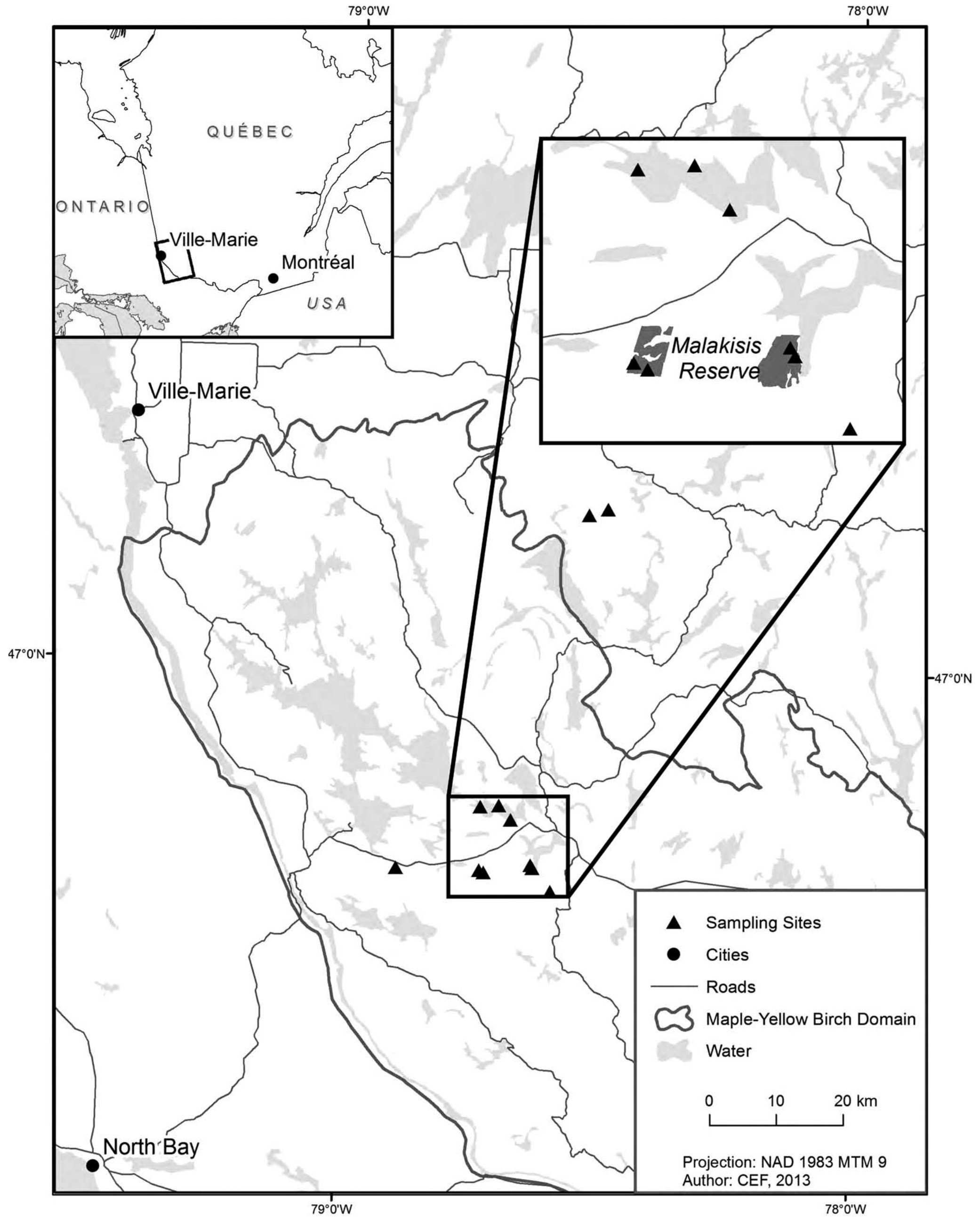

**Figure 1. Location of the sampling plots in the Temiscamingue region. The inset in the upper right corner is an enlargement of the zone surrounding the Lake-Malakisis Ecological Reserve (shown in dark gray).**

**Table 1. Total number of trees (one core per tree) used for dendrochronological analysis for each species, combining individuals from all 11 plots, time span covered, and interseries correlation.**

| | No. of trees | Time span | Interseries correlation |
|---|---|---|---|
| Sugar maple | 570 | 1742–2011 | 0.172 |
| Yellow birch | 108 | 1751–2011 | 0.203 |
| Balsam fir | 60 | 1896–2011 | 0.384 |
| Red maple | 28 | 1913–2011 | 0.408 |
| White spruce | 15 | 1900–2011 | 0.489 |

observed dbh distributions to theoretical negative exponential, logistic, and two- and three-parameter Weibull distributions (Goodburn and Lorimer 1999, Zhang et al. 2001) and used Kolmogorov-Smirnov tests to assess distribution fits. The logistic function was used to describe a rotated sigmoid distribution. Statistical analyses were performed in R (R Core Team 2014), using the *fitdistrplus* package to calculate the theoretical dbh distributions (Delignette-Muller et al. 2013). The Akaike information criterion corrected for small sample size (AICc) was used to select the best-fitting model. Tree recruitment patterns were visually explored using age distributions.

### Spatial Structure

Gap dynamics is a stochastic process that should lead to spatial randomness (Petritan et al. 2013). To test the hypothesis of spatial randomness of age, dbh, and species, we recorded the spatial coordinates of trees within each plot and performed a spatial point pattern analysis on continuous (dbh and age) and discrete (species and dead trees) variables, also known as "marks" (Stoyan and Stoyan

**Table 2. Number of trees, density, and basal area for living and dead trees in each plot.**

| | | Living trees | | | Dead trees | | |
|---|---|---|---|---|---|---|---|
| Sample plot | Age (yr) | No. | Density (stems/ha) | Basal area ($m^2$/ha) | No. | Density (stems/ha) | Basal area ($m^2$/ha) |
| SP5 | 99 | 93 | 372 | 18.9 | 53 | 212 | 8.7 |
| SP11 | 111 | 102 | 408 | 24.6 | 45 | 180 | 7.7 |
| SP10 | 117 | 95 | 380 | 24.3 | 32 | 128 | 18.7 |
| SP3 | 119 | 87 | 348 | 22.9 | 24 | 96 | 3.8 |
| SP9 | 129 | 77 | 308 | 27.7 | 35 | 140 | 7.0 |
| SP6 | 134 | 132 | 528 | 22.4 | 72 | 288 | 11.8 |
| SP8 | 147 | 93 | 372 | 18.6 | 24 | 96 | 9.2 |
| SP7 | 151 | 66 | 264 | 22.4 | 22 | 88 | 8.2 |
| SP2 | 167 | 94 | 376 | 22.1 | 18 | 72 | 17.5 |
| SP1 | 184 | 89 | 356 | 20.4 | 28 | 112 | 12.0 |
| SP4 | 195 | 82 | 328 | 24.0 | 41 | 164 | 6.9 |

Sample plots are sorted by minimum age using the 90th percentile of the ages of dated trees.

**Table 3. Importance value of each species by sample plot for all living trees.**

| Sample plot | Acsa | Beal | Abba | Tsca | Acru | Pigl | Thoc | Bepa | Osvi | Quru | Pogr | Pist |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SP5 | 15.44 | 39.68 | 25.98 | | 17.58 | | | | | | 1.33 | |
| SP11 | 77.08 | 18.27 | 1.13 | | 1.25 | 1.71 | | | | | | 0.56 |
| SP10 | 70.93 | 25.61 | 1.44 | | 0.59 | 1.43 | | | | | | |
| SP3 | 54.60 | 29.59 | 7.46 | 0.73 | 1.16 | 5.26 | 1.20 | | | | | |
| SP9 | 75.86 | 8.74 | | 7.69 | | | 7.72 | | | | | |
| SP6 | 8.13 | 63.49 | 16.51 | 2.91 | 0.45 | 1.42 | 0.92 | 6.17 | | | | |
| SP8 | 62.92 | 33.44 | | | | 1.31 | | | | 2.32 | | |
| SP7 | 77.22 | 7.77 | | 15.01 | | | | | | | | |
| SP2 | 94.88 | 3.55 | | | | | | | 1.57 | | | |
| SP1 | 90.22 | 5.28 | | | | | | | 2.95 | 1.54 | | |
| SP4 | 36.72 | 46.21 | 10.63 | 2.14 | 2.16 | 2.14 | | | | | | |

Sample plots are sorted by minimum age. Acsa, *Acer saccharum* Marsh.; Beal, *Betula alleghaniensis* Britton; Abba, *Abies balsamea* (L.) Mill.; Tsca, *Tsuga canadensis* (L.) Carrr.; Acru, *Acer rubrum* L.; Pigl, *Picea glauca* (Moench) Voss; Thoc, *Thuja occidentalis* L.; Bepa, *Betula papyrifera* Marsh.; Osvi, *Ostrya virginiana* (Mill.) K. Koch; Quru, *Quercus rubra* L.; Pogr, *Populus grandidentata* Michx.; Pist, *Pinus strobus* L.

1994, Illian et al. 2008). We used the translation correction to account for edge effects (Illian et al. 2008, Grabarnik et al. 2011). All plots were under similar climatic and topographic conditions and, thus, were considered homogeneous (i.e., stationary) and isotropic. We further assumed that plot location had no effect on the point patterns. For quantitative marks (age and dbh), we used the mark-weighted $L$ function $L_{mm}(r)$, which is the square root transformation of the mark-weighted $K$ function $K_{mm}(r)$ (Penttinen et al. 1992, Illian et al. 2008, Grabarnik et al. 2011) used to stabilize the variance (Illian et al. 2008, Grabarnik et al. 2011). The mark-weighted $L$ function tests for mark independence, which corresponds to random labeling, and indicates stimulation or inhibition between marks. Stimulation indicates that neighboring trees have a larger dbh (or are older) than the mean stand dbh (or age), whereas inhibition indicates that neighboring trees have a smaller dbh (or are younger) than the mean stand dbh (or age) (for details, see Illian et al. 2008).

For qualitative marks (species and dead trees), we used the $L$ function $L(r)$ to test for attraction or repulsion. For the species variable, the $L$ function was only calculated for plots with at least 30 individuals of the same species (Aakala et al. 2012). We tested the complete spatial randomness (CSR) hypothesis of marked Poisson point processes by using Monte Carlo goodness-of-fit simulations and deviation tests (Loosmore and Ford 2006, Grabarnik et al. 2011). We computed 999 simulations to approximate $\alpha = 0.05$ (Grabarnik et al. 2011).

Because sample size was low within each individual plot, we used replicated point pattern analysis using all plots combined to validate the results that were obtained from single plots (Illian et al. 2008). Aggregated summary characteristics were calculated by simple averaging, because all plots were of the same dimensions (Illian et al. 2008). We calculated 999 Monte Carlo simulations and deviation tests of these aggregated estimators, as described previously (Loosmore and Ford 2006, Grabarnik et al. 2011). Spatial statistical analyses were performed within R (R Core Team 2014), using the *spatstat* package (Baddeley and Turner 2005).

## Results

### Species Composition

Stand age, as described by the 90th percentile of the aged trees, varied from 99 to 195 years, but trees that were older than 200 years were present in all but two plots. The number of living trees and tree density varied among plots (Table 2). The basal area of living trees varied to a lesser degree and ranged between 18.6 and 27.7 $m^2$/ha across all plots (Table 2). Mean $\pm$ SD crown area was 87.5 $\pm$ 69.7 $m^2$ for dominant sugar maple and 100.0 $\pm$ 71.3 $m^2$ for dominant yellow birch, corresponding to crown diameters of 10.6 and 11.3 m, respectively. Sugar maple and yellow birch had high importance values in all plots; three plots were dominated by yellow birch and the other eight were dominated by sugar maple (Table 3). Yellow birch importance values tended to decrease with stand age, whereas the opposite trend was observed for sugar maple. For stands that were dominated by yellow birch (plots 4, 5, and 6), tree species composition was similar regardless of stand age, whereas for those stands that were dominated by sugar maple (in addition to yellow birch), balsam fir, and red maple (*Acer rubrum* L.) were present in stands that were younger than 120 years, and white spruce (*Picea*

**Table 4. Comparison of dbh distributions with theoretical distributions (negative exponential, logistic, and two- and three-parameter Weibull) for each sample plot.**

| | Negative exponential | | Logistic | | Two-parameter Weibull | | Three-parameter Weibull | |
|---|---|---|---|---|---|---|---|---|
| Sample plot | *D* | *P* | *D* | *P* | *D* | *P* | *D* | *P* |
| SP5 | 0.15 | 0.024* | 0.25 | <0.001* | 0.09 | 0.445 | 0.09 | 0.375 |
| SP11 | 0.10 | 0.256 | 0.13 | 0.064 | 0.09 | 0.391 | 0.07 | 0.678 |
| SP10 | 0.07 | 0.769 | 0.17 | 0.010* | 0.07 | 0.807 | 0.06 | 0.846 |
| SP3 | 0.11 | 0.269 | 0.13 | 0.090 | 0.07 | 0.795 | 0.08 | 0.557 |
| SP9 | 0.10 | 0.422 | 0.11 | 0.344 | 0.08 | 0.727 | 0.08 | 0.724 |
| SP6 | 0.10 | 0.150 | 0.11 | 0.077 | 0.07 | 0.483 | 0.08 | 0.420 |
| SP8 | 0.19 | 0.002* | 0.23 | <0.001* | 0.13 | 0.090 | 0.14 | 0.064 |
| SP7 | 0.08 | 0.773 | 0.16 | 0.069 | 0.09 | 0.721 | 0.07 | 0.904 |
| SP2 | 0.12 | 0.119 | 0.17 | 0.008* | 0.09 | 0.485 | 0.08 | 0.615 |
| SP1 | 0.1 | 0.386 | 0.19 | 0.004* | 0.06 | 0.948 | 0.06 | 0.946 |
| SP4 | 0.07 | 0.777 | 0.18 | 0.012* | 0.06 | 0.904 | 0.07 | 0.774 |

Only living individuals with dbh ≥9.1 cm were included in the analysis. *D* is the value of the Kolmogorov-Smirnov statistic. Sample plots are sorted by minimum age.
*The observed data were considered to be statistically different from the theoretical distribution.

**Table 5. AICc values for logistic, exponential, and two-parameter Weibull and three-parameter Weibull distributions for each sample plot.**

| | AICc | | | |
|---|---|---|---|---|
| Sample plot | Logistic | Exponential | Two-parameter Weibull | Three-parameter Weibull |
| SP5 | 1,180.24 | 1,068.43 | 1,062.73 | 997.56* |
| SP11 | 1,286.49 | 1,237.11 | 1,236.93 | 1,235.98* |
| SP10 | 1,217.61 | 1,147.79 | 1,149.83 | 1,130.87* |
| SP3 | 1,103.02 | 1,062.62 | 1,060.50 | 1,060.12* |
| SP9 | 1,004.37 | 982.31 | 977.77* | 979.30 |
| SP6 | 1,573.68 | 1,544.23 | 1,527.93 | 1,527.44* |
| SP8 | 1,183.39 | 1,080.64 | 1,079.51 | 1,036.08* |
| SP7 | 872.69 | 827.27 | 829.37 | 821.50* |
| SP2 | 1,201.61 | 1,130.10 | 1,132.10 | 1,116.18* |
| SP1 | 1,134.43 | 1,061.59 | 1,063.53 | 1,048.14* |
| SP4 | 1,068.97 | 1,007.40 | 1,009.45 | 991.00* |

The lowest AICc values indicate the best fits.
*Lowest AICc value for each sample plot.

*glauca* [Moench] Voss), eastern white cedar, and eastern hemlock were present in 120- to 160-year-old stands. Eastern hop-hornbeam (*Ostrya virginiana* [Mill.] K. Koch) and red oak (*Quercus rubra* L.) were present in stands that were older than 160 years (Table 2). For stands that were dominated by sugar maple, tree species diversity decreased with age ($t = -2.50$, $df = 6$, $P = 0.047$).

### Stand Structure

Nine of the 11 stands had their dbh distribution follow a negative exponential, and all followed a two- or three-parameter Weibull function (Table 4). In comparison, only 5 of the 11 plots were well fitted by a logistic function (Table 4). A goodness-of-fit test showed that the three-parameter Weibull function was always the best theoretical function for describing the dbh structure, except for sample plot (SP) 9, which was better fitted by a two-parameter Weibull function (Table 5). Tree recruitment was continuous through time, occurring almost every decade in all stands (Figure 2). Most stands showed recruitment pulses that were centered around 1920–1930 AD and 1870–1880 AD, but a few stands (plots 7 and 10) showed a more constant pattern of recruitment (Figure 2).

### Spatial Structure

The mark-weighted *L* function for tree age showed random labeling for 10 of the 11 plots (Table 6). A significant spatial structure was only detected for plot 7 (inhibition, indicating a uniform distribution) (Figure 3A). The replicated point pattern analysis for age-confirmed independence, which corresponded to random labeling (Table 6). The spatial structure of dbh did not follow random labeling in three plots where inhibition patterns were found (plots 1, 5, and 7; Figure 3B–D), and two other plots were close to the significance level (plots 3 and 9) (Table 6). The replicated point pattern analysis confirmed inhibition at ~6–13 m (Figure 3E). The distribution of tree species showed CSR, and those results were confirmed by the replicated point pattern analysis (Table 6).

### Spatial Structure of Dead Trees

The number and density of dead trees and snag basal area varied from one plot to another (Table 2). The mean ± SD fraction of dead trees as a percentage of total trees (living + dead) was 27.2 ± 6.6%. In stands that were dominated by sugar maple, there were fewer dead trees in older plots than in younger plots (Table 7). The spatial structure of dead trees followed CSR in all plots (Table 7). The replicated point pattern analysis confirmed CSR (Table 7).

## Discussion

### Stand Composition

Along the minimum age span of the 11 plots (~100–200 years), we detected a change in species composition, particularly in stands that were dominated by sugar maple (Table 3). Based on Hubbell (2001), we hypothesized that in a quasi-equilibrium state equivalent to the old-growth temperate deciduous forests that we sampled, stochastic recruitment processes would cause new tree species to arrive with time. However, tree species richness decreased instead of increasing, contrary to our hypothesis. Higher species richness in younger stands was associated mainly with the presence of short-lived species such as balsam fir and red maple. Our study only focused on tree species, and we could not verify for possible temporal changes in species richness for other taxa (shrubs, herbs, and mosses, among others).

### Stand Structure

Old-growth temperate deciduous forests are often assumed to be characterized by a rotated sigmoid (logistic) dbh distribution at equilibrium (Goodburn and Lorimer 1999, Lorimer et al. 2001),

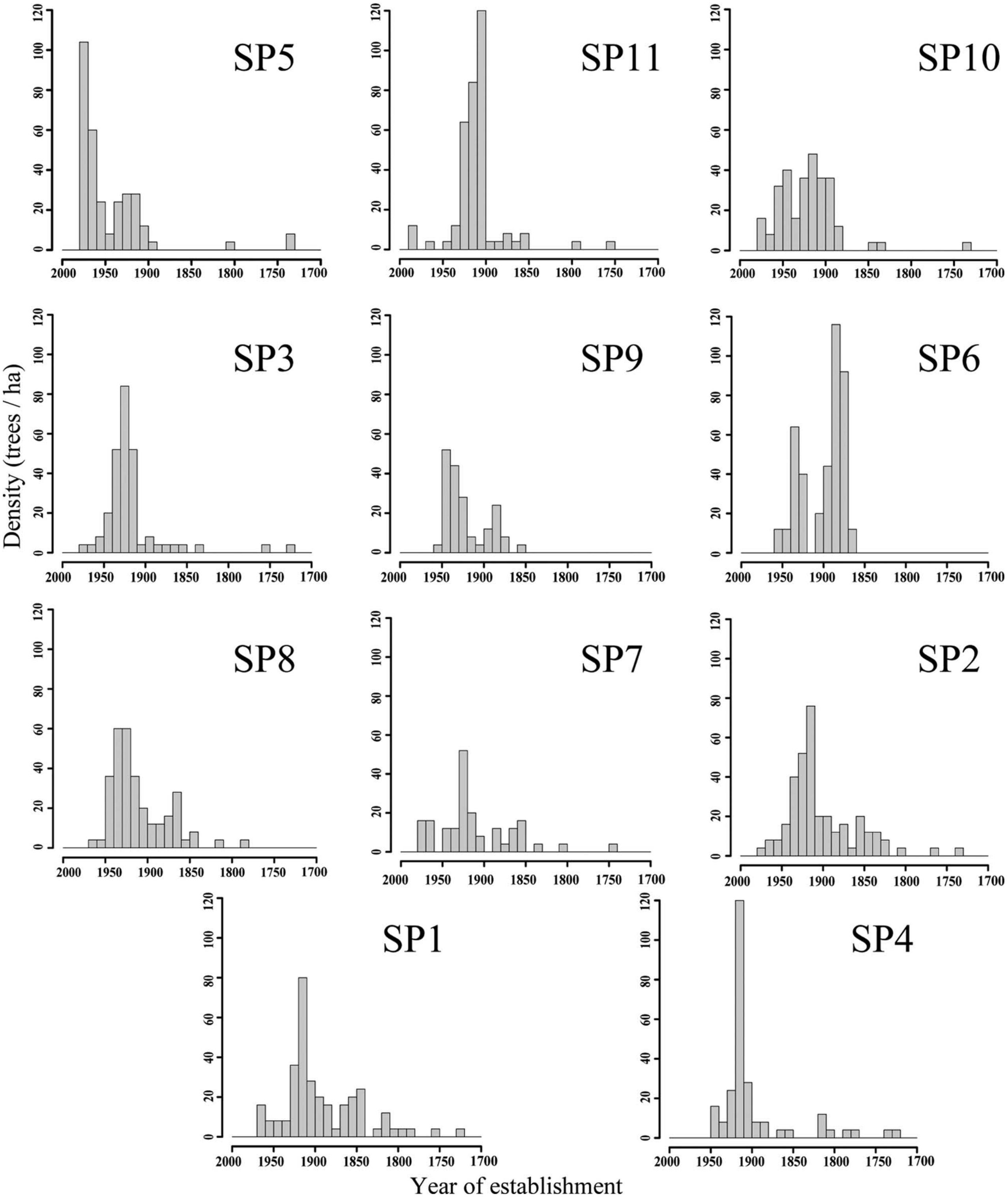

**Figure 2. Tree (dbh ≥ 9.1 cm) age structure for each sampling plot. Plots are sorted by minimum age from upper left to lower right.**

with a U-shaped pattern representing high mortality of small suppressed trees, low mortality of vigorous canopy trees, and high mortality of large senescent trees (Runkle 2000, Rubin et al. 2006). However, in our study area, size distributions of all stands were well fitted to the negative exponential distribution or to a two- or three-parameter Weibull function, but not to a logistic distribution (Figure 4). The Weibull function is a generalized function that could represent a negative exponential distribution (Westphal et al. 2006). The goodness-of-fit test showed that the three-parameter Weibull was the best theoretical function for describing the dbh structure (except for SP9 which was better fitted by a two-parameter Weibull function), contrary to our hypothesis that the oldest stands would follow a rotated sigmoid distribution. This unexpected result could be explained by the location of the study sites at the northern range limit of temperate deciduous forests, which are characterized by cooler climatic conditions and a faster stand replacement period that is due to smaller and more frequent gaps (Payette et al. 1990).

A high proportion of dead trees was found in all plots compared with that in mature temperate deciduous stands (Burrascano et al. 2013). In stands that were dominated by sugar maple, the proportion of dead trees decreased with stand age. Perhaps the mortality rate was lower in the older stands because they were at or near equilibrium (Tyrrell and Crow 1994). This response needs to be investigated further, considering the importance of deadwood and snags in old-growth temperate deciduous forests (Hodge and Peterken 1998, Burrascano et al. 2008, Wirth et al. 2009).

**Table 6. Deviation from mark independence corresponding to random labeling of age and dbh and CSR of species for living trees in old-growth temperate deciduous forests of western Quebec.**

| | *u* | | | | |
|---|---|---|---|---|---|
| | | | Species | | |
| Sample plot | Age: $L_{mm}(r)$ | Dbh: $L_{mm}(r)$ | $L_{\text{Acsa}}(r)$ | $L_{\text{Beal}}(r)$ | $L_{\text{Abba}}(r)$ |
| SP5 | 77.96 | 177.79* | | | 8.38 |
| SP11 | 2.17 | 20.00 | 0.22 | | |
| SP10 | 23.17 | 5.50 | 1.26 | | |
| SP3 | 12.83 | 106.71† | 7.40† | | |
| SP9 | 7.29 | 60.84† | 0.63 | | |
| SP6 | 1.96 | 18.35 | | 1.55 | 6.87 |
| SP8 | 5.95 | 38.30 | 4.17† | | |
| SP7 | 130.72* | 123.53* | 5.35 | | |
| SP2 | 10.77 | 7.31 | 2.50 | | |
| SP1 | 6.82 | 89.58* | 2.06 | | |
| SP4 | 37.43 | 53.94 | 1.84 | | |
| Replicated | 1.32 | 35.45‡ | 17.89 | | 17.89 |

Sample plots are sorted by age (90th percentile). For quantitative marks (age and dbh), the mark-weighted *L* function $L_{mm}(r)$ was used. For discrete marks (species) the *L* function $L(r)$ was computed. Acsa, sugar maple; Beal, yellow birch; Abba, balsam fir. *u*, value of the Diggle-Cressie-Loosmore-Ford test of the CSR statistic.
$^*P < 0.05$.
$^†P < 0.1$.
$^‡P < 0.01$.

### Weibull Size Distribution as a Strange Attractor

The study stands usually showed continuous recruitment, which is consistent with both our hypothesis and gap phase dynamics (Fraver et al. 2009). However, recruitment was generally not constant, and pulses were recorded around 1870–1880 AD in 4 of the 11 stands and around 1920–1930 AD in 8 of the 11 stands (Figure 2). Recruitment pulses could result from intermediate disturbances such as windstorms or from the harvesting of large white pines (*Pinus strobus* L.) at the end of the 19th and at the beginning of the 20th century (Vincent 1995, Roy et al. 2010). Indeed, the pulse recorded at the end of the 19th century could correspond to the establishment of the first sawmill in the study area in 1874 AD (Vincent 1995). The pulse at the beginning of the 20th century could correspond to a series of natural intermediate disturbances, including a spruce budworm (*Choristoneura fumiferana* Clem.) outbreak in 1910 AD and fires between 1921 and 1923 AD, as well as the intensification of white pine harvesting (Grenier et al. 2005, Drever et al. 2006).

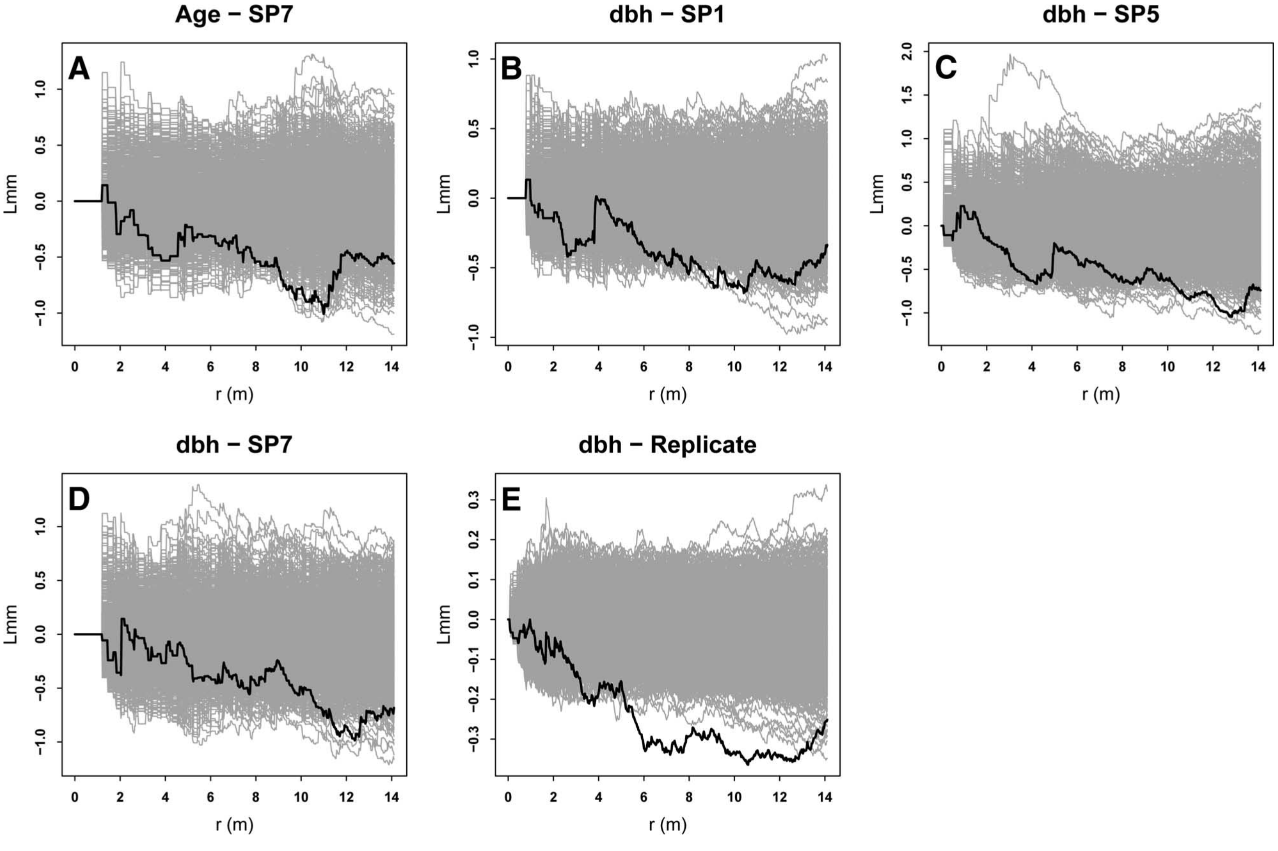

Figure 3. Mark-weighted *L* function for age (SP7; A) and dbh (SP1, SP5, and SP7 and replicate; B, C, D, and E, respectively) as a function of radius (in m). The black line corresponds to the observed $L_{mm}$ value and each gray line to one of the 999 Monte Carlo simulations of the envelope test. Negative $L_{mm}$ values outside the envelope represent inhibition, whereas positive $L_{mm}$ values outside the envelope represent aggregation. $L_{mm}$ values within the envelope limit represent random labeling. Note that these figures are not statistically reliable because it is impossible to control for type I error of the envelope test. They should only be used as a guide to interpret the results of the deviation test.

Although recruitment patterns (continuous versus pulse) differed among plots, dbh structures all converged toward a two- or three-parameter Weibull distribution. Indeed, the signal of intermediate disturbances that was seen in the age structures (recruitment pulses) was lost in the dbh distributions. It often has been suggested that a negative exponential or a Weibull size distribution involves constant recruitment and mortality (e.g., Niklas et al. 2003, Rubin et al. 2006). Obviously, forests rarely follow these premises for a long time. Our results suggest that intermediate disturbances can modify the rate of recruitment and that growth and mortality vary with size classes, as has been reported elsewhere (Bédard and Majcen 2003, Fortin et al. 2008).

**Table 7. Deviation from CSR for the spatial structure of dead trees in old-growth temperate deciduous forests of western Quebec, from *L* function *L*(*r*).**

| Sample plot | $\%_{\text{dead trees}}$ | *u* | *P* |
|---|---|---|---|
| SP5 | 36.3 | 2.25 | 0.47 |
| SP11 | 30.6 | 2.46 | 0.59 |
| SP10 | 25.2 | 2.17 | 0.86 |
| SP3 | 21.6 | 10.88 | 0.46 |
| SP9 | 31.5 | 2.12 | 0.84 |
| SP6 | 35.3 | 0.37 | 0.93 |
| SP8 | 20.5 | 19.00 | 0.22 |
| SP7 | 25.0 | 3.35 | 0.94 |
| SP2 | 16.1 | 19.66 | 0.44 |
| SP1 | 24.4 | 14.64 | 0.18 |
| SP4 | 33.3 | 4.10 | 0.42 |
| Replicated | 28.1 | 11.08 | 0.93 |

Sample plots are sorted by age (90th percentile). $\%_{\text{dead trees}}$, percentage of dead trees (in density); *u*, value of the Diggle-Cressie-Loosmore-Ford test of CSR.

As an alternative mechanism for explaining the convergence in dbh structure for forests with different recruitment histories, we suggest that the temporally variable and spatially heterogeneous light environment that was generated by gap dynamics in old-growth temperate deciduous forests offers a wide range of growth conditions. This allows trees of the same age to grow into different size classes while aging, with many growing slowly under low light conditions and a few growing quickly under prolonged favorable light conditions. This growth difference generates a Weibull dbh distribution. For example, in our study area, a sugar maple with a 30-cm dbh could equally be 70 or 180 years old (data not shown). Under such dynamics, forests can experience different disturbance histories, but they all converge toward the same structural archetype, which acts like a strange attractor (Roberts 1996). Such chaotic determinism has been understood to commonly emerge in natural forest systems that are subject to gap dynamics (Crawley and Ross 1990, Wu and Loucks 1995, Stone and Ezrati 1996).

### Tree Spatial Structure

Neither the mark-weighted *L* function for age nor the *L* function for species demonstrated any specific spatial pattern (Table 6). The spatial distribution of dead trees was also random within all plots (Table 7). This lack of spatial structure in tree spatial patterns supports our hypothesis that gaps in temperate deciduous forests are small and occur randomly (Frelich and Graumlich 1994, Chokkalingam and White 2001, Curzon and Keeton 2010). However, the mark-weighted *L* function for dbh did not show random labeling (Table 6); rather, it indicated inhibition at ~6–13 m distances. This range includes the mean crown size of dominant sugar maple and yellow birch trees (crown diameters of 10 and 11 m, respectively).

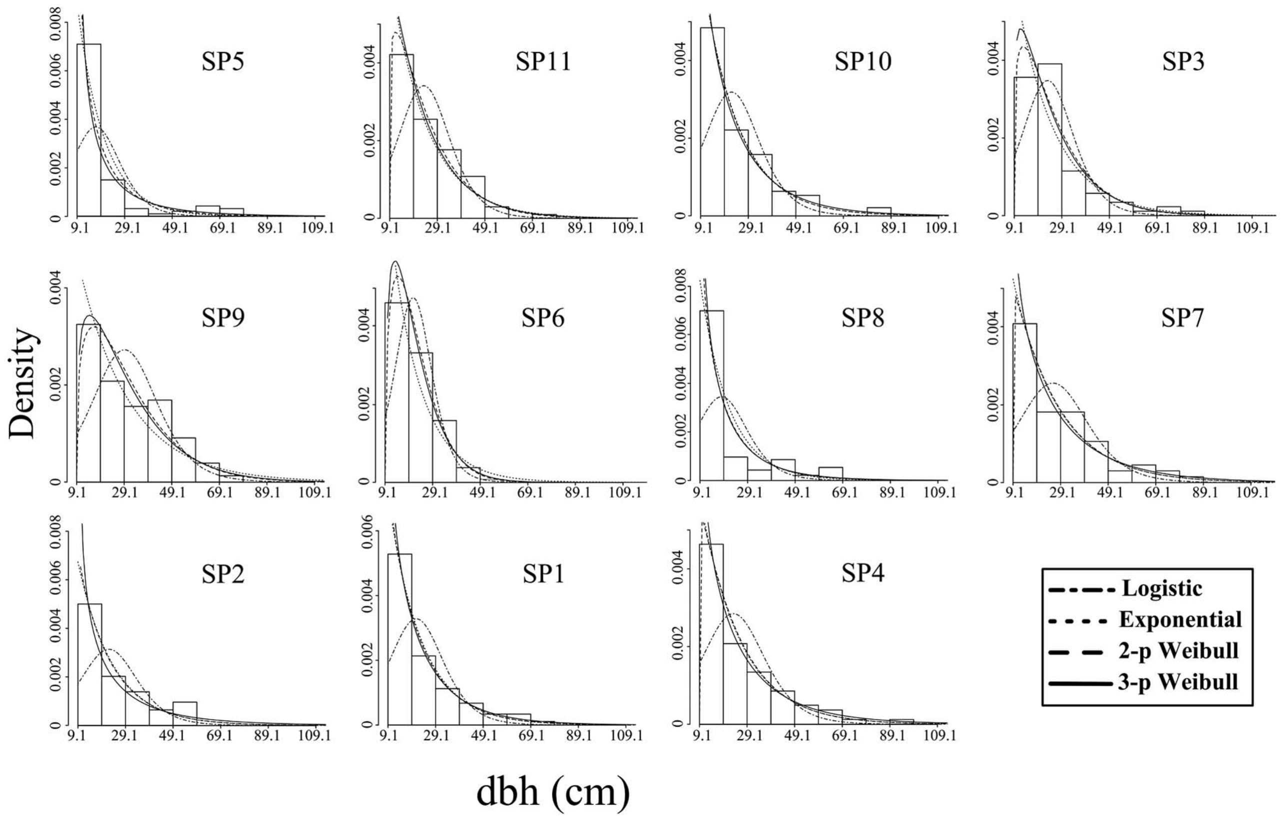

**Figure 4. Theoretical distributions (logistic, exponential, and two- and three-parameter Weibull) fitted to dbh density distributions for each sample plot. Plots are sorted by minimum age from upper left to lower right.**

Thus, small suppressed trees are over-represented at the boundary of two dominant crowns, which is probably due to higher light availability (Messier et al. 2009). Random gap occurrence creates a heterogeneous light environment under the forest canopy that varies with time. The footprint that is created by randomness persists with age, but not with diameter, providing further evidence of the "strange attractor" process that was described in the previous section.

## Conclusion

In this study, we found that the structural characteristics of old-growth temperate deciduous forests were different in several ways at the northern limit of their range compared with more central locations. First, species richness did not increase with age (Hubbell 2001), although species composition did vary. This finding supports the current practice of tree marking in the study area, where short-lived companion species to sugar maple (e.g., balsam fir and red maple) are planned to be harvested first. Second, the age structure of some stands did show constant recruitment as expected (Fraver et al. 2009), but other stands showed recruitment pulses, possibly indicative of intermediate disturbances. This finding suggests that selection silviculture should occasionally include larger, multiple-tree gaps in addition to single-tree gaps (Hanson and Lorimer 2007). Third, no shift in diameter distributions from a Weibull to a rotated sigmoid was observed (Lorimer et al. 2001, Westphal et al. 2006). Hence, selection cutting across the range of diameter classes does not seem to be a problem in our study area, in contrast to other regions where it would fail to recreate the rotated sigmoid distribution (Goodburn and Lorimer 1999). Fourth, spatial randomness was observed for age, species, and dead trees, which supports various harvest levels across harvesting blocks (Keeton 2006, North and Keeton 2008). Further research is needed to attain a better understanding of old-growth temperate deciduous forests at their northern distribution limit, most notably with respect to the estimation of disturbance rates.

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