

Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems

Mike R. Saunders and Robert G. Wagner

Abstract: Using inventory data from a long-term silviculture experiment in east-central Maine, spatial models were developed to analyze 28 years (1974–2002) of stand structural dynamics. Differences in spatial pattern, species mingling, height differentiation, and relative stand complexity index (rSCI) were compared among five treatments: commercial clear-cutting, fixed diameter-limit, 5 year single-tree selection, three-stage shelterwood (both with and without precommercial thinning), and unharvested natural areas. Regardless of treatment, regeneration events (whether induced by natural breakup of the overstory or by harvesting) increased aggregation in spatial pattern and reduced species mingling, more so in the commercial clearcut and fixed diameter-limit treatments where hardwood densities were highest. Regular spatial patterns were rare. Height differentiation values for individual trees and stand-level mean rSCI were generally highest in untreated natural areas and 5 year selection treatments, intermediate in commercial clearcut and fixed diameter-limit treatments, and lowest in three-stage shelterwood treatments. After a brief adjustment period, precommercial thinning in a shelterwood treated stand generally increased species mingling, height differentiation, and rSCI. Two untreated natural areas exhibited divergent pathways of structural development. Dynamics in uneven-aged selection treatments more closely resembled that of the untreated natural areas than did the shelterwood, commercial clearcut, or fixed diameter-limit treatments.

Résumé : En utilisant les données d'inventaire d'une expérience sylvicole à long terme dans le centre-est de l'État du Maine, aux États-Unis, des modèles spatiaux ont été mis au point pour analyser la dynamique de la structure du peuplement pendant une période de 28 ans (1974 à 2002). Les différences de patron spatial, de mélange d'espèces, de différenciation de la hauteur et d'indice relatif de complexité des peuplements (ICPr) ont été comparées parmi cinq traitements : la coupe à blanc commerciale, la coupe à diamètre limite fixe, la coupe de jardinage par pied d'arbre selon une rotation de cinq ans, la coupe progressive d'ensemencement en trois étapes (avec et sans éclaircie commerciale) et des peuplements naturels non coupés. Indépendamment du traitement, l'établissement de la régénération (induit par la sénescence naturelle des arbres dominants ou par la coupe) augmentait l'agrégation des patrons spatiaux et diminuait le mélange des espèces et ce, de façon plus marquée dans la coupe à blanc commerciale et dans la coupe à diamètre limite où la densité des espèces feuillues était la plus forte. Les patrons spatiaux réguliers étaient rares. Les valeurs de différenciation de la hauteur des arbres individuels et d'ICPr moyen à l'échelle du peuplement étaient généralement plus élevées dans les peuplements naturels non traités et dans la coupe de jardinage selon une rotation de 5 ans, intermédiaires dans la coupe à blanc commerciale et dans la coupe à diamètre limite, et plus faibles dans la coupe progressive d'ensemencement en trois étapes. Après une brève période d'ajustement, l'application d'une éclaircie précommerciale dans un peuplement soumis à la coupe progressive augmentait généralement le mélange des espèces, la différenciation de la hauteur et l'ICPr. Deux peuplements naturels non traités montraient des trajectoires divergentes de développement de la structure. La dynamique dans les coupes de jardinage appliquées à des structures inéquiennes était plus près de celle des peuplements naturels non traités que ne l'étaient la coupe progressive d'ensemencement, la coupe à blanc commerciale ou la coupe à diamètre limite fixe.

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Introduction

Maintenance and creation of stand structural complexity through silvicultural intervention has become a dominant

theme in forest management in recent years, both to protect ecosystem function and to conserve biodiversity (Schütz 1999; O'Hara 2001; Franklin et al. 2002; Palik et al. 2002; Zenner 2004). Silvicultural removal of trees can increase or decrease species diversity, change spatial pattern among stems or species, and (or) change the size distribution of trees within the stand (Buongiorno et al. 1994; Sendak et al. 2003; Montes et al. 2005). For example, some traditional approaches to even-aged regeneration methods (i.e., clearcut, uniform shelterwood, and seed-tree harvests) that do not retain legacy structures can homogenize stand structure and, when applied broadly in some ecosystems over time, can reduce landscape-level biodiversity (Seymour and Hunter 1999; O'Hara 2001; Lindenmayer and Franklin 2002). Fur-

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M.R. Saunders.¹ Purdue University, Department of Forestry and Natural Resources, 715 W. State Street, West Lafayette, IN 47907-2061, USA.

R.G. Wagner. University of Maine, School of Forest Resources, 5755 Nutting Hall, Orono, ME 04469-5755 USA.

¹Corresponding author (e-mail: msaunder@purdue.edu).

ther, intermediate treatments used within these same even-aged silvicultural systems can sometimes increase, but more often reduce, structural diversity by removing undesirable species and redistributing growing space more uniformly among residual stems (Seymour and Hunter 1999; Homyack et al. 2004). Uneven-aged stands are thought to retain high amounts of structural diversity, but in fact, may lead to stand structures as artificial as those created with even-aged methods (O'Hara 1996; Seymour and Kenefic 1998; Schütz 1999), especially if natural disturbance regimes are dominated by stand-replacing events and (or) if the selection system does not explicitly maintain snags and coarse woody material.

The effects of silviculture on stand structure have traditionally been quantified by changes in species composition, basal area, stand density, and (or) stem diameter distributions. Although these variables can be important when assessing the sustainability of forest ecosystems (O'Hara et al. 2007), they do not adequately describe the complexity of stand structure (Zenner 2004). For example, von Gadow and Hui (1999) demonstrated that theoretical stands with identical basal areas, densities, and diameter distribution, but differing spatial arrangements, can have vastly different structures that affect future stand dynamics and silvicultural options.

In a spatially explicit context, forest stand structure can be described using three components: (i) spatial pattern or positioning of tree stems, (ii) amount of mingling or intermixing of tree species, and (iii) degree of size differentiation among neighbors (Pommerening 2002; Aguirre et al. 2003; Kint et al. 2003). Of the three components, spatial pattern has been most widely studied, often in late-successional or old-growth stands, and has been linked to resource availability, regeneration ecology, and competition theory (Phillips and MacMahon 1981; Kenkel 1988; Skarpe 1991; Mast and Veblen 1999). Species mingling and size differentiation have been far less studied, generally being confined to identifying the scale at which species pairs or size-classes are attracted or repulsed by one another (Peterson and Squiers 1995; Mast and Veblen 1999).

During the development of even-aged stands, these three components change in predictable ways. During stand establishment (*sensu* Oliver and Larson 1996), regeneration processes generally lead to aggregated stands with low degrees of species mingling and size differentiation. Heterogeneous site conditions and (or) disturbances that leave residual trees from the previous stand tend to increase mingling and size differentiation. As competition increases during stem exclusion, the pattern can become more uniform (Phillips and MacMahon 1981; Kenkel 1988), with mingling increasing or decreasing depending on the grain of site heterogeneity, and size differentiation becoming more constant. Lastly, as stands enter understory reinitiation and progress toward old-growth stages of development, overall spatial pattern across broad scales may again become clustered as regeneration increases in canopy gaps (Armesto et al. 1986; North et al. 2004), but the spatial pattern among the original cohort at short spatial scales will usually remain random or slightly regular as density-independent mortality increases (Szwagrzyk and Czerwczak 1993). Mingling and size differentiation will likely increase during these stages as new species and cohorts become established in the understory.

Although numerous studies have described the spatial pattern in forests, relatively few have tracked the long-term dynamics of these patterns over time or accessed the effect of different silvicultural treatments on spatial indices. Some studies have used temporary sample plots to examine a chronosequence or several discrete stages of stand development (Franklin et al. 2002; Grassi et al. 2003; Zenner 2004), but these approaches have generally ignored the history of individual stands (Montes et al. 2005). Many studies have reconstructed spatial patterns by mapping live and dead stems, and using dendrochronological techniques to date mortality events (Harrod et al. 1999; Mast and Veblen 1999; Motta and Edouard 2005). Inference about spatial patterns in these studies, however, is often limited to the largest size-classes of trees, since smaller size-classes have decayed and are not represented in stem reconstructions. Repeated measurement of permanent plots is ideal, particularly if the measurements are frequent enough to document silvicultural entries or natural disturbance events. However, such data sets are rare (O'Hara et al. 2007), particularly at the larger scales (≥ 0.5 ha) used in most spatial analyses (e.g., Peterson and Squiers 1995; Ward et al. 1996).

This study focused on the structural development of mixedwood stands in the Acadian ecoregion of North America. Using stem mapping and modeling with a morphing algorithm (Saunders 2006), the spatial-explicit structure of 50 repeatedly measured inventory plots was reconstructed from a long-term silvicultural experiment in east-central Maine. We quantified differences in structural development over a 28 year period for stands treated with commercial clear-cutting, fixed diameter-limit harvesting, 5 year single-tree selection, three-stage shelterwood (both with and without precommercial thinning), and unharvested natural areas. We hypothesized that

- (1) spatial pattern after any harvest treatment will be more aggregated for both small and large trees than in the unmanaged stands, but without further disturbance the spatial pattern in each stand will become more regular over time;
- (2) species mingling will be higher in unmanaged stands and stands with uneven-aged structures (selection) than even-aged management (shelterwood) or exploitative harvesting (commercial clearcut or diameter-limit); and
- (3) size differentiation will be higher in unmanaged and uneven-aged stands than in either even-aged stands or stands with exploitative harvesting.

In addition, we also assessed the utility of the stand complexity index (SCI; Zenner and Hibbs 2000) for integrating spatial pattern and size differentiation. We hypothesized that the SCI (as originally described) would be highest in unmanaged and uneven-aged stands, lowest under even-aged management, and intermediate with exploitative harvesting.

Methods

Study area

This study took place on the Penobscot Experimental Forest (PEF) near Bradley, Maine (44°49'30"N, 68°38'00"W). The PEF lies in the Acadian Forest, an ecotone between the boreal forest of Canada and northern hardwood forests of

southern New England. Climate is cool and humid with mean temperatures ranging from -7.7 °C in January to 20.0 °C in July, and precipitation averaging 106 cm, approximately half of which falls as snow (Brissette 1996; Sendak et al. 2003). Soils are derived from glacial till and range from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams and silt loams in flat areas between the ridges.

Forest types within the PEF are primarily mixedwoods, but usually dominated by Acadian region softwoods (Sendak et al. 2003), including red spruce (*Picea rubens* Sarg.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), and northern white-cedar (*Thuja occidentalis* L.). Associated hardwood species include red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), gray birch (*Betula populifolia* Marsh.), quaking aspen (*Populus tremuloides* Michx.), and bigtooth aspen (*Populus grandidentata* Michx.). Sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), northern red oak (*Quercus rubra* L.), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), and basswood (*Tilia americana* L.) are more common on higher quality sites.

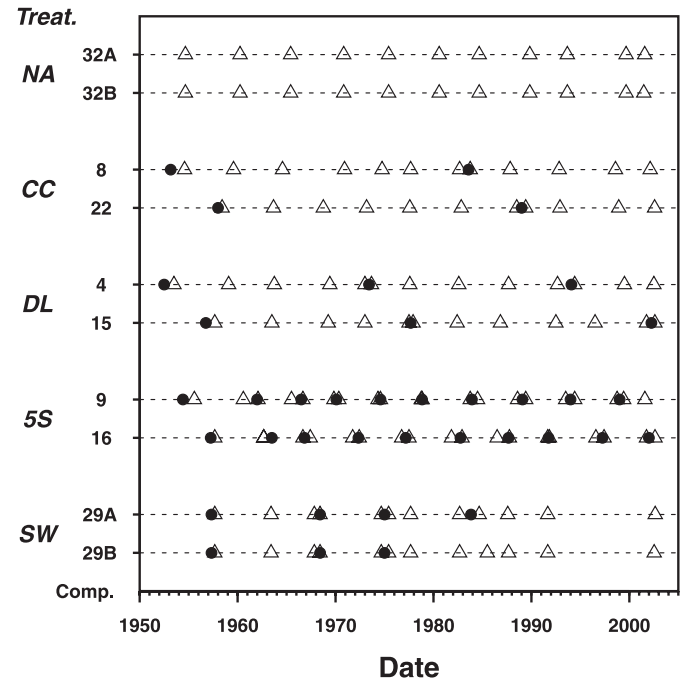
The typical structure of natural stands in the Acadian forest are irregularly uneven aged resulting from partial canopy disturbances, such as senescence, wind, ice storms, pathogens, and insect herbivory. Disturbance frequencies average 0.7%–1.3% per year (Runkle 1982; Seymour et al. 2002). Large-scale, stand-replacing disturbances, such as fire or major wind events, have return intervals of 250–800 years or more (Lorimer 1977).

Long-term silvicultural experiment

From 1952 to 1957, the USDA Forest Service (USFS) installed a replicated study to investigate the influences of silviculture and exploitive harvesting practices on the composition, growth, yield, and structure of mixed northern conifer stands (Sendak et al. 2003). Eight treatments were randomly assigned to one of sixteen 6.6–17.5 ha compartments: 5, 10, and 20 year single-tree selection systems, two- and three-stage uniform shelterwood systems, fixed and flexible diameter-limit harvests, and unregulated commercial clear-cutting. In the early 1980s, both three-stage shelterwood compartments were divided to investigate the influence of precommercial thinning (PCT) on stand development. In addition, an unmanaged natural area was later set aside as a “pseudo-control” for the experiment; this compartment was divided in 1993 after it developed into two distinct stands. Detailed prescriptions, harvest techniques, and timings for each treatment are described by Sendak et al. (2003).

The history of the PEF before 1950 is not well documented, but the forest was probably irregularly uneven aged as a result of natural stand development confounded with periodic partial harvesting (Sendak et al. 2003). A sawmill operated within the boundaries of the forest throughout much of the 1800s; pine and spruce were likely preferentially harvested from much of the forest during this period.

Fig. 1. Inventory dates (\triangle) and harvest entries (\bullet) for the 10 compartments used in this study. Silvicultural treatments included an unmanaged natural area (NA), commercial clear-cutting (CC), fixed diameter-limit harvesting (DL), 5 year single-tree selection (5S), and three-stage shelterwood (SW). Compartment 29 was divided into 29A and 29B in 1983 to compare precommercial thinning (29A) with no thinning (29B).



The spruce budworm epidemic of 1913–1919 also had a significant influence on pretreatment species composition (Seymour 1992). Regardless, initial conditions throughout much of the northern half of the PEF were relatively constant, differing only slightly by the domination of spruce–fir or hemlock in the initial stocking inventories (Sendak et al. 2003). Therefore, nearly all changes in species composition and structure can be attributed to subsequent treatment effects (J. Brissette, personal communication, 2006).

Tree inventories have been conducted within compartments before and after every cutting treatment and approximately every 5 years thereafter (Fig. 1). A systematic grid (with a random start) of 8–21 permanent sample points is located within each compartment. Stem diameter and condition of all trees >11.4 cm diameter at breast height (DBH = 1.35 m) were measured within 0.081 ha (0.2 acre) circular plots; saplings between 1.2 and 11.4 cm DBH were measured in a concentric 0.020 ha (0.05 acre) circular subplot (Sendak et al. 2003). Beginning in 1974, individual trees and saplings within each plot were labeled using a systematic numbering scheme creating a longitudinal record of tree growth and mortality.

Field measurements

This study focused on structural development within 10 compartments that included one of five treatments: commercial clear-cutting, fixed diameter-limit harvesting, 5 year single-tree selection, three-stage shelterwood (both with and without precommercial thinning), and unharvested natural

Table 1. Number of locations and relocation rates for management compartments of the natural area (NA), 5-year selection (5S), three-stage shelterwood (SW), fixed-diameter limit (DL), and commercial clearcut (CC).

Treatment	Compartment	Locations			Relocation rates (% of)		
		Living	Dead	Unknown	Total	Dead	Dead >11.4 cm DBH
NA	32A	1268	194	64	95.8	75.2	81.7
	32B	309	79	20	95.1	79.8	88.0
5S	9	394	205	175	77.4	53.9	75.8
	16	422	154	128	81.8	54.6	75.5
SW	29A	891	72	401	70.6	15.2	42.9
	29B	1625	336	59	97.1	85.1	80.0
DL	4	814	314	362	75.7	46.4	79.0
	15	410	255	241	73.4	51.4	73.3
CC	8	888	326	800	60.3	29.0	41.6
	22	962	307	646	66.3	32.2	47.8

Note: Low relocation rates in compartment 29A are primarily the result of the precommercial spacing treatment that occurred in 1981.

areas. Prior USFS inventories and cutting entries for these compartments are shown in Fig. 1.

From June 2001 through August 2002, the spatial location of 10 225 trees and saplings (both living and dead) were mapped for five nested overstory and sapling permanent sample plots in each compartment (50 plots total). These mapped plots were randomly selected from all USFS inventory plots in a compartment with the restriction that chosen plots must be at least 20 m away from any permanent access road wherever possible. Dead tree or sapling positions were recorded by comparing stump locations and diameters to past USFS numbered tree lists for that plot; this located from 15% to 85% of all dead stems, depending on compartment (Table 1). Azimuths were determined using a hand compass, and distances from plot center were measured with a Haglöf DME (Haglöf 2003). Positional errors increased with distance from plot center, but were generally no more than 0.25 m. Diameter at breast height was measured to the nearest 0.1 mm with either metal tape or calipers (for trees too small for conventional metal tapes), and condition (i.e., cull, declining, leaning stem, etc.) was recorded. Crown radii in quadrants defined by the four cardinal directions were measured to the nearest 0.1 m using a metal tape. Total tree or sapling height and the lowest live branch (continuous to the upper crown) were measured to the nearest 0.1 m either directly, using 10 and 15 m telescoping height poles, or as an average of two to four readings from a Haglöf hypsometer (Haglöf 2002).

Spatial reconstruction model

Three steps were used to reconstruct the structural development of stands in each compartment. First, height development of all past and current trees and saplings on each plot had to be calculated from the field measurements, as previous inventories had not measured height. We used the multilevel, mixed-effects models of Saunders and Wagner (2008) for the more common tree species. For the remaining species, the Chapman–Richards growth function was fit

$$[1] \quad HT = 1.35 + a[1 - e^{(bDBH)}]^c + \varepsilon$$

where HT is tree height (m), DBH is tree diameter at breast height (cm), a , b , and c are estimated parameters, and $\varepsilon \sim N(0, \phi)$, with generalized nonlinear least-squares (GNLS)

regression to develop species and species group relationships. For all undamaged living trees, we then smoothed deviations from the mean height development pattern by defining a modified proportional adjustment (MPA) that would allow individual trees to grow proportionally more or less than the average tree or sapling models. Reconstructed heights were as follows

$$[2] \quad HT_i^* = MPA(HT_i - 1.35) + 1.35$$

where HT_i^* is the adjusted height prediction of the tree or sapling in inventory i , HT_i is the predicted height in inventory i from the species-specific or group-specific height equations, and

$$[3] \quad MPA = (HT_{obs} - 1.35)/(HT_{pred} - 1.35)$$

where HT_{obs} is the observed tree or sapling height and HT_{pred} is the predicted tree or sapling height using the DBH measured in this study. Dead and unlocated trees and saplings were assumed to follow the mean height development patterns and, therefore, did not use MPA. Trees and saplings with broken tops were also assumed to follow mean height development patterns until they reached HT_{obs} .

The next step was simulating the location of all trees and saplings from previous inventories that could not be relocated during field measurements. Tree-numbering protocols used in previous inventories were systematic based on azimuth, distance from plot center, and tree size. This numbering system allowed us to narrow the simulation of an unknown tree to a relatively small area (~ 5 – 30 m²) within subplots or plots, but required the assumption of isotropy for analysis. Additional details of the algorithm used to simulate unknown positions of trees can be found in Saunders (2006).

The last step in model development was to scale the sapling subplot (0.020 ha) up to that of the tree plot (0.081 ha). We used a modified version of the morphing algorithm (Williams et al. 2003; Saunders 2006) to remap the locations of the sapling plot from the Euclidean space C with origin (0,0) and radius of r ($=8.05$ m) to a square space D of equal area and a side length of $r\pi^{0.5}$. The normal morphing algorithm was followed by torodial wrapping D with copies of itself to create a 3×3 array. This array was then “demorphed” back to Euclidean space to a circle of radius $3r$ and that could be trimmed to any scale between r and $3r$.

Table 2. Spatially explicit indices used in this study.

Index	Purpose	Equation	Source
Modified Clark–Evans statistic (CE)	Spatial pattern	$CE = \frac{r_A}{r_E} = \frac{\frac{1}{N} \sum_{i=1}^N r_i}{0.5 \left(\frac{A}{N}\right)^{1/2} + 0.0514 \frac{P}{N} + 0.041 \frac{P}{N^{3/2}}}$	Clark and Evans (1954); Donnelly (1978)
Mingling index (DM _{<i>i</i>})	Pattern interspersion of discrete marks (species)	$DM_i = \frac{1}{3} \sum_{j=1}^3 V_{ij}$	von Gadow and Hui (1999)
Differentiation index (TH _{<i>i</i>})	Pattern interspersion of continuous marks (size)	$TH_i = \frac{1}{3} \sum_{j=1}^3 \left[1 - \frac{\min(S_i, S_j)}{\max(S_i, S_j)} \right]$	von Gadow and Hui (1999)
Stand complexity index (SCI)	Structural variability	$SCI = \sum_{i=1}^n \frac{ a_i \times b_i }{2} / A_T$	Zenner and Hibbs (2000)

Note: r_A , actual mean nearest neighborhood distance in plot; r_E , expected mean nearest neighborhood distance assuming complete spatial randomness; r_i , distance between tree i and its nearest neighbor; N , total number of trees; A , plot area; P , plot perimeter; V_{ij} , 1 if tree i and j th nearest neighbor are different species, 0 otherwise; $S_{[i]}$, size mark of tree i or j th nearest neighbor; A_T , total ground area within Delaunay triangulation of tree positions, excluding triangles of edge trees that may have nearest neighbor outside the plot; and $|a_i \times b_i|$, the absolute value of the product of vector AB with coordinates $a_i = (x_{ib} - x_{ia}, y_{ib} - y_{ia}, z_{ib} - z_{ia})$ and vector AC with coordinates $b_i = (x_{ic} - x_{ia}, y_{ic} - y_{ia}, z_{ic} - z_{ia})$, where $x_{[i]}$ and $y_{[i]}$ are x and y coordinates of tree i and $z_{[i]}$ is a continuous mark (e.g., a size variable).

We deviated from the normal algorithm in two ways. First, we randomly selected with replacement all subplots (C_i) within the same management compartment as the focal subplot for torodial wrapping within the algorithm; in other words, D could now be wrapped with copies of itself or with any other D_i from that compartment. Saunders (2006) reported that this technique was superior to the normal morphing algorithm for multiple plot analysis, generally reducing the regularity brought into the simulated pattern as normally happens with torodial wrapping. Second, all C_i values were rotated before morphing by adding a random azimuth to locations. This approach reduced the chance that the same “side” of a subplot would be used again during the wrapping procedure, thereby further reducing induced regularity in the simulated pattern. However, the rotation also required an assumption of isotropy in the pattern and analysis.

Statistical analysis of structural dynamics

Spatial indices

We used an array of spatially independent variables (basal area, stand density, species composition, and diameter distribution) to summarize the temporal changes among compartments and treatments. We also chose one spatially dependent index each to summarize changes in pattern, mingling, and size differentiation; including the modified Clark–Evans nearest neighborhood index (CE), the mingling index (DM), and the size (height) differentiation index (TH), respectively. In addition, the SCI was calculated to characterize three-dimensional physiognomic (i.e., positional) structure (Table 2).

The Clark–Evans nearest neighbour index is a ratio of the mean nearest neighbor distances in any spatial pattern (r_A) to that mean distance (r_E) expected under complete spatial randomness (csr; Table 2). The Clark–Evans nearest neighbour index ranges from 0 for completely aggregated points to 1 for csr to 2.1491 for perfectly regular hexagonally distributed points. Significances of departure of CE from csr were tested with a standard, normal variate defined as

$$[4] \quad c = \frac{r_A - r_E}{\sigma_{r_E}} \quad \text{where } \sigma_{r_E} = \frac{0.26136}{\sqrt{N\lambda}}$$

where N is the number of points and λ is the density of the point pattern (Clark and Evans 1954).

The mingling index and TH measure the interspersion of either discrete or continuous marks within a point pattern, respectively (Table 2). Following Pommerening (2002) and Kint et al. (2003), both are defined using a four-neighbor structural group and are calculated as point-level variables that range from 0 to 1. This approach allows both DM and TH to be summarized either as frequency distributions or means for either the entire pattern or a subpopulation of points within the pattern. In this study, DM was used to estimate mingling within a point pattern using tree species as a discrete mark, whereas TH was used to estimate size differentiation by using tree height as the continuous mark. Low mean DM values, therefore, suggested a lack of species diversity within the pattern and (or) that individual species formed a highly segregated and clumped distribution within the pattern. Conversely, high mean DM values suggested more species diversity and (or) that individual species were regularly distributed and formed a more complete mixture in the point pattern (Kint et al. 2003). Plots with low mean TH values had little height differentiation and indicated a uniform and potentially even-aged structure. Subpopulations with a low TH indicated that they were subordinate to most of their neighbors and that these subpopulations were most likely to occur in lower crown classes or strata within the stand (Aguirre et al. 2003; Kint et al. 2003). The distributional properties of DM and TH were not known, but permutation approaches can be used to test for significant differences between the observed values and that of a random mixture of mark proportions and point locations as the observed pattern (Kint et al. 2003).

The SCI integrates tree positioning and size variation as a measure of structural variability (Table 2). The SCI is calculated by first creating a Delaunay triangulation of the spatial positions of the trees within a plot, with the restriction that triangles along the edge of the two-dimensional triangulation

are omitted if they may have a closest neighbor outside the plot. Size attributes associated with each tree can then be attached to the two-dimensional triangulation to form a ragged triangulation surface in three (or more) dimensions. The SCI is then defined as the ratio of surface area of three-dimensional triangulation to that of the two-dimensional triangulation. The distributional statistics for SCI under various spatial and tree size distributions are not known. The SCI has a lower limit of 1 when all trees are the same size (Zenner and Hibbs 2000). The SCI does not appear to have an upper limit, as trial simulations have shown SCI to increase dramatically with increasing tree density and the range in size among the trees (Saunders et al. 2002; McElhinny et al. 2005).

Summarizing and testing spatial indices

The randomness of the simulation procedure in the reconstruction models—in particular, the simulation of missing tree and sapling locations and the scaling of sapling subplots—required a permutation-based approach for summarizing and testing with the spatial indices. Therefore, 100 realizations of the complete spatial pattern (i.e., a “master” list of all known and unknown locations) were simulated for each plot. For each realization, spatial pattern was held constant across inventories by simply trimming out all trees not measured during an inventory from the master list of locations. Realizations that had $n < 5$ were discarded from further analysis, since several of the spatial indices were unstable at such small sample sizes.

All spatial indices were summarized by compartment and inventory period. The estimator for the mean value of any given index (\bar{I}) was calculated as a weighted average of all realizations within a compartment following Diggle (2003)

$$[5] \quad \bar{I} = \frac{\sum_{i=1}^p \sum_{j=1}^{r_p} n_{ij} I_{ij}}{\sum_{i=1}^p \sum_{j=1}^{r_p} n_{ij}}$$

where p is the number of plots in a compartment, r_p is the realization for each plot p , and n is the number of trees in realization r of plot p . The sampling variance of \bar{I} was estimated from 1000 bootstrapped samples of \bar{I}^* defined as

$$[6] \quad \bar{I}^* = \sum_{k=1}^p n_k I_k / \sum_{k=1}^p n_k$$

where the I_k are sampled at random with replacement from all $i \times j = k$ realizations in the compartment (Diggle 2003). Bootstrapped 95% confidence intervals were calculated using ± 1.96 SE of \bar{I}^* . For CE, these bootstrapped 95% confidence intervals were tested against csr of a simulated plot of mean density for each compartment in a particular inventory. Permutation-based tests of DM and TH against a random mixture hypothesis were not conducted, since it would have required separate testing for each realization of each plot (i.e., an infeasible 3.8×10^7 resamples). All model development and testing used R (R Development Core Team 2005) with contributed packages nlme (Pinheiro et al. 2006), spatstat (Baddeley and Turner 2005), splan (Rowlington et al. 2005), spdep (Bivand et al. 2006), and trimesh (Gebhardt et al. 2006).

Lastly, the overall structural development of the compartments was summarized using nonmetric multidimensional

scaling (NMS) of the plot means of basal area, density, hardwood importance (% hardwood density \times % hardwood basal area), size-class distribution, CE, DM, TH, number of stems with $TH_i \geq 0.6$ and $TH_i < 0.6$, and SCI_r . Each variable was standardized by the norm (Greig-Smith 1983), and Sørensen distances were used. A random starting configuration was used with a step-down dimensionality algorithm on 40 runs of the real data. A Monte Carlo test using 50 runs of randomized data was used to assess the probability of obtaining a more stable solution by chance. All NMS analyses were conducted with PC-ORD[©] 4.07 (McCune and Melford 1999) with the Kruskal–Mather algorithm (Kruskal 1964; Mather 1976; McCune and Grace 2002).

Results

Stand characteristics and size structure

Traditional stand metrics (basal area and stem density) captured some differences in the structural development patterns among treatments (Fig. 2). Basal area and density trends showed the typical decline and subsequent regrowth after harvest entries for all four treatments. Both replicates of each treatment generally responded the same to harvest, but were staggered in time based on different harvest timings.

A notable exception was in the two natural areas (NA) where a clear divergence in structure was evident. Beginning about 1980, the proportion of balsam fir basal area and density increased dramatically within compartment 32A and then continued to decline in compartment 32B (Figs. 3 and 4). The high proportion of small saplings suggests that compartment 32A experienced a significant regeneration event (Fig. 5), likely following the loss of overstory balsam fir from the spruce budworm epidemic of the late 1970s. In contrast, compartment 32B had relatively constant species composition, with hemlock gradually replacing balsam fir over time (Figs. 3 and 4).

The commercial clear-cut and fixed-diameter limit treatments produced an irregular structure with species composition shifting from domination by spruce, fir, and hemlock at the beginning of the experiment in the 1950s and moving towards hardwood species (Fig. 4). This trend was evident by 1975 and accelerated following the second harvest entries during the 1980s. There also was a buildup of larger diameter cedar in three of the four compartments for these treatments, as indicated by a disproportionately large basal area relative to density (Figs. 3 and 4). As expected, these stands also had few trees in sawtimber size-classes (Fig. 5).

The 5 year single-tree selection treatment maintained a relatively stable species composition over 28 years, although there was a gradual replacement of balsam fir with hemlock in both density and basal area (Figs. 3 and 4). This treatment maintained a wider diameter distribution than other treatments (Fig. 5). The wide error bars for density and basal area estimates (Fig. 2) suggested that horizontal variability in the single-tree selection treatment was high, perhaps related to the skid trail network used in previous harvests.

Both three-stage shelterwood (SW) compartments received final removal cuts in 1974, prior to the inventories analyzed in this study. Since all residual stems ≥ 6.4 cm DBH were removed in this harvest, these compartments ex-

Fig. 2. Basal area and stem density for all stems >1.2 cm DBH by compartment for the unmanaged natural area and four silvicultural treatments from 1974 to 2002. Rapid declines in basal area and density indicate a harvest. Error bars indicate ± 1 SE.

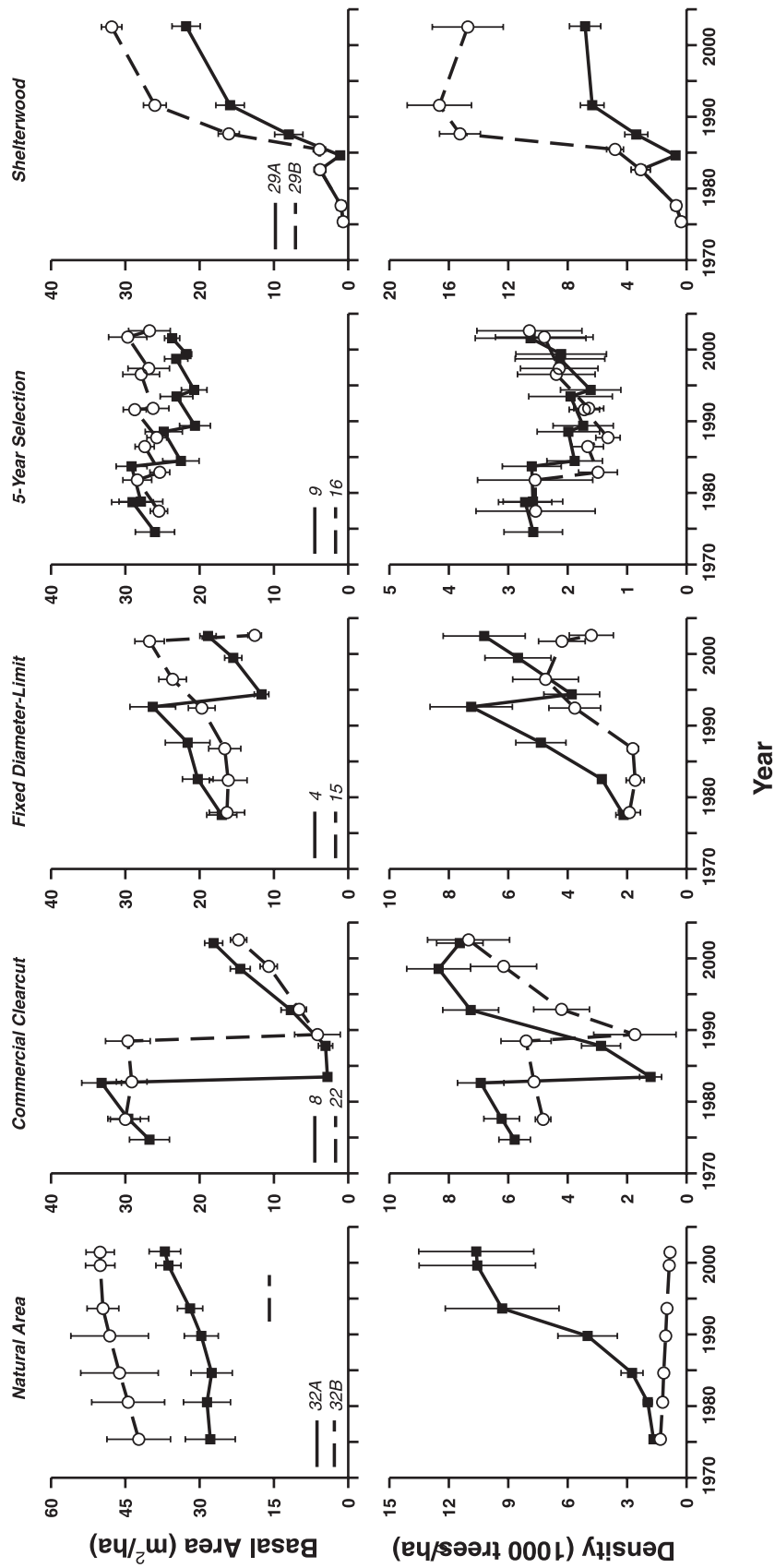


Fig. 3. Proportion of basal area by species or species group for the unmanaged natural area and four silvicultural treatments by compartment from 1974 to 2002.

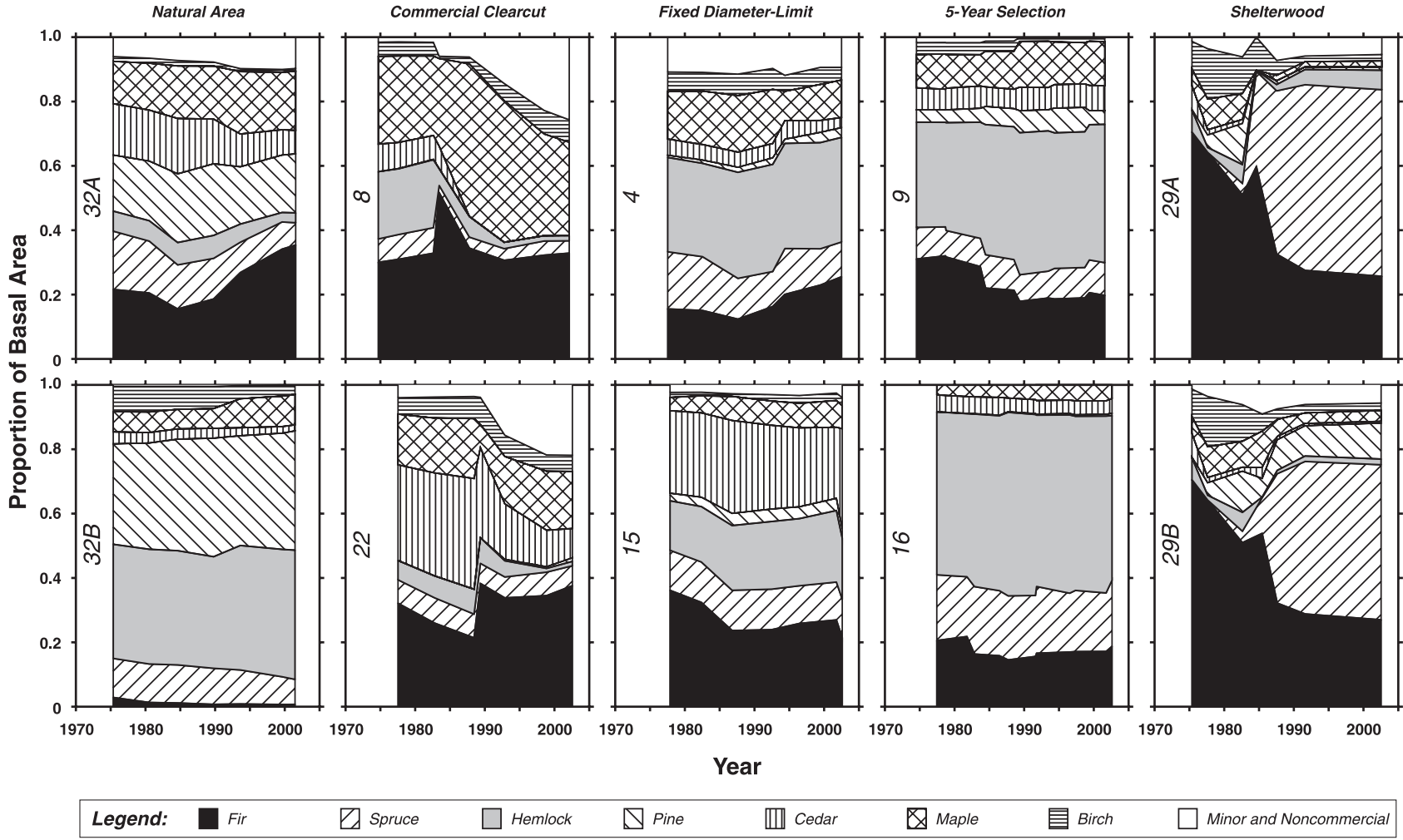


Fig. 4. Proportion of density by species or species group for the unmanaged natural area and four silvicultural treatments by compartment from 1974 to 2002.

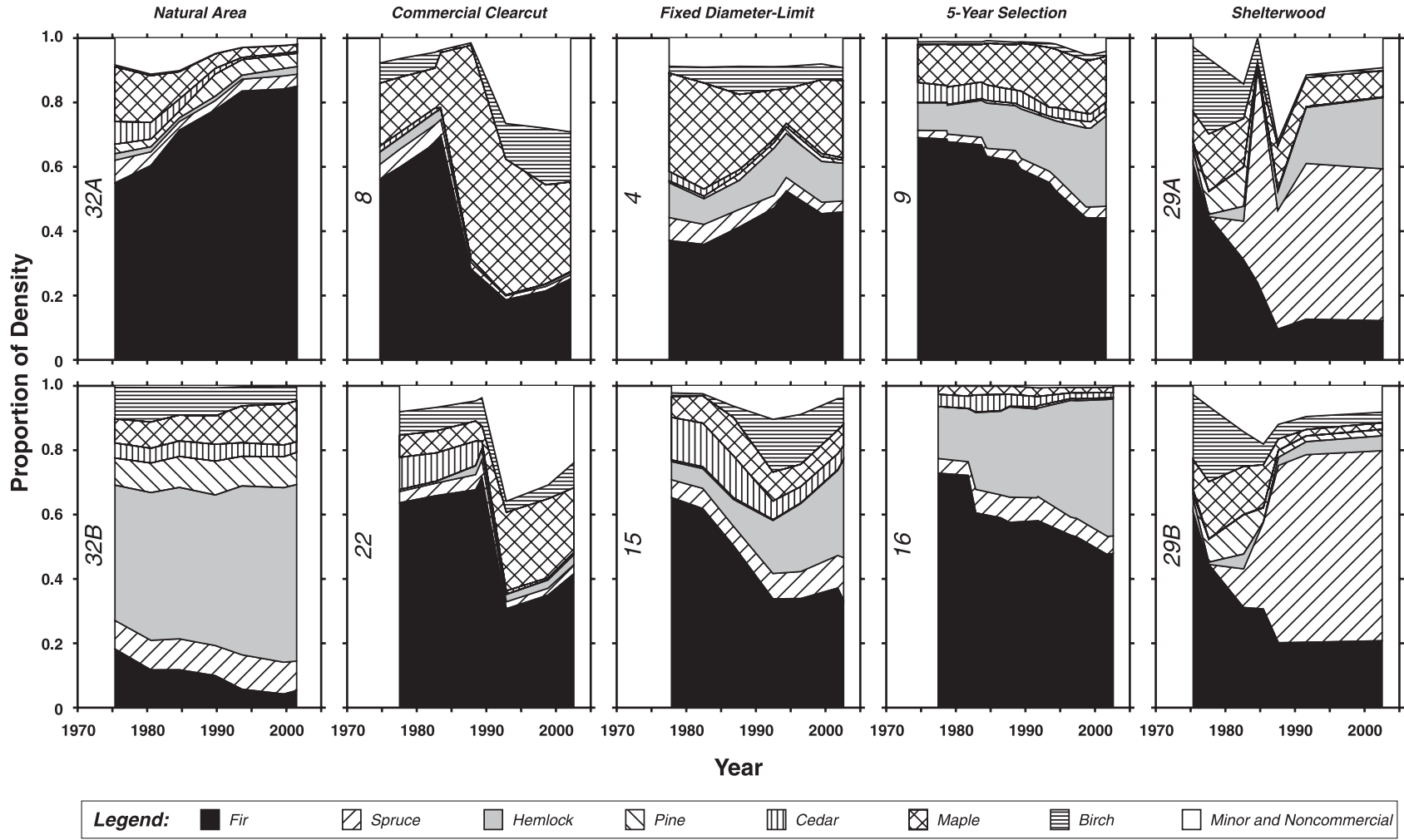
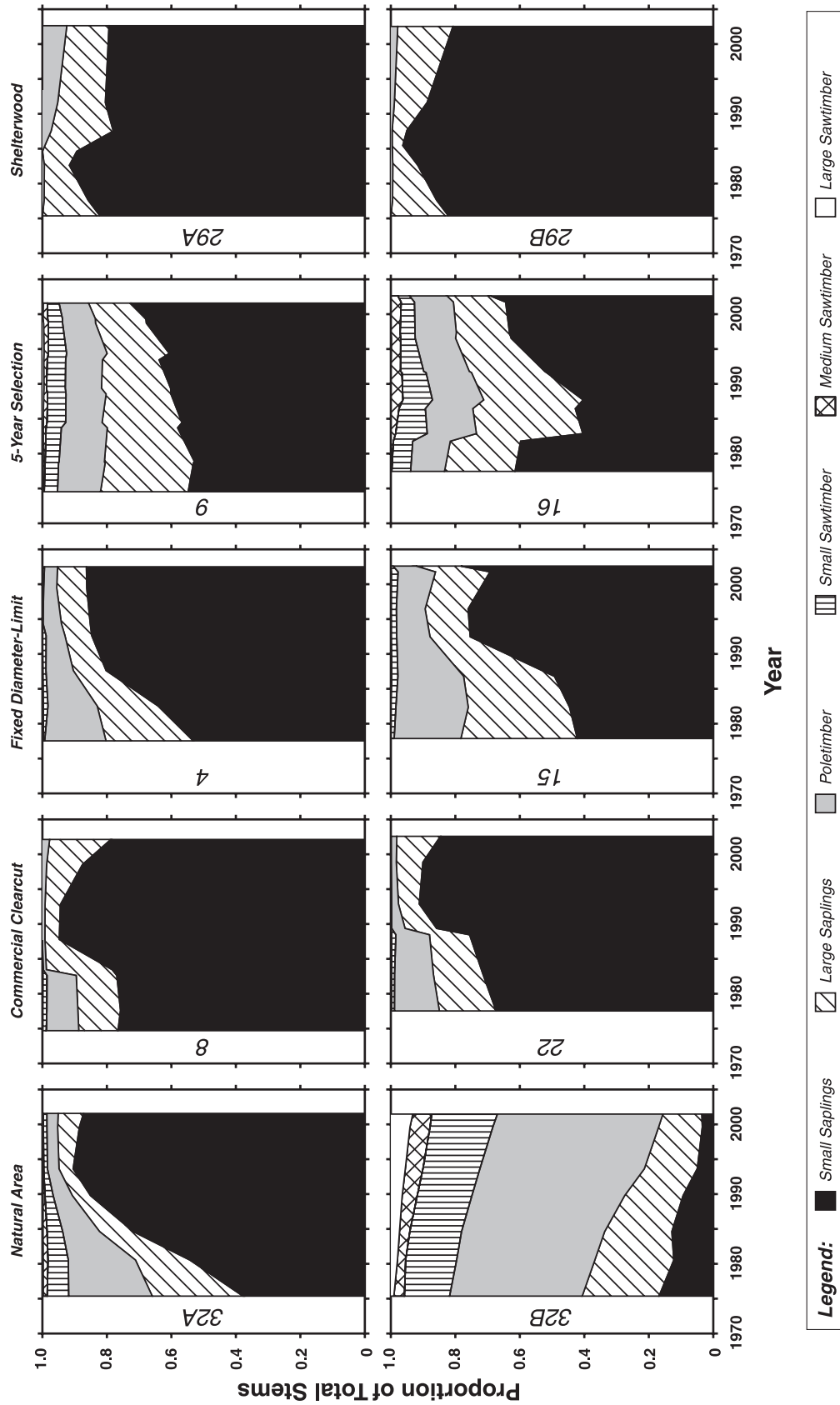


Fig. 5. Shifts in diameter distributions for the unmanaged natural area and four silvicultural treatments by compartment from 1974 to 2002. Size groupings are defined by diameter as small saplings, 1.2–6.3 cm; large saplings, 6.4–12.7 cm; poletimber, 12.8–25.4 cm; small sawtimber, 25.5–38.1 cm; medium sawtimber, 38.2–50.8 cm; and large sawtimber, >50.9 cm.



perienced a standwide regeneration event and have since developed along typical even-aged pathways, with both density and basal area increasing as regeneration grew into the inventory (Fig. 2). In contrast with the other treatments, the species composition was dominated by spruce and fir, with the PCT during 1983 within compartment 29A further increasing dominance by these species (Figs. 3 and 4). By reducing competition and increasing individual tree growth, PCT also increased the proportion of stems in poletimber size-classes relative to compartment 29B, which did not receive PCT (Fig. 5).

Spatial patterning

Treatments differed dramatically in spatial patterning as measured by CE. When saplings and trees were considered together, CE values indicated an aggregated pattern ($p < 0.05$) for all compartments except for compartment 32B and compartment 16 from 1981 to 1991 (Fig. 6a). Regeneration events, whether triggered naturally (compartment 32A) or by harvesting, immediately reduced CE values. Differences in the amount of decline in CE among compartments may be attributed to the harvest treatments used and (or) the density of hardwoods in the preharvest stand, as these increased the proportion of stump sprouts relative to seed-origin seedlings in subsequent inventories (Fig. 4).

When trees only with DBH >11.4 cm were considered, however, the spatial pattern rarely ($p < 0.05$) departed from *csr*. Aggregation was only detected for trees in three of the four compartments that were treated by commercial clear-cutting or fixed diameter-limit harvesting: compartment 4, compartment 15 during the 1986 and 2000 inventories, and compartment 8 for all inventories after 1990 (Fig. 6b). In these treatments, harvesting appeared to increase aggregation of larger individuals over time.

Species mingling

Mingling among species appeared to be determined primarily by the relative proportion of hardwood and softwood species within the spatial pattern (Fig. 7a). Mean DM values were intermediate to low (0.4–0.6) for most treatments. Commercial clear-cutting, fixed diameter-limit harvesting, and PCT tended to reduce mingling immediately after harvest; likely because these treatments would have selected for certain species. Regeneration events appeared to further reduce species mingling, suggesting that regeneration by any given species was clumped in space (e.g., hardwood sprouting) or time (e.g., conifer masting). Compartment 32B stands out with a relatively high DM value, likely owing to a long period without significant regeneration.

As a group, hardwood species had higher DM values than softwood species in most treatments (Figs. 7b and 7c). Hardwood species were less common in most stands and more dispersed, particularly in the older age stands. Harvesting had a larger effect on hardwood DM values, presumably because of stump sprouting and root suckering by these species. Softwood species had DM values similar to that of whole stands, because softwood species made up the majority of stems (Figs. 7a and 7c).

Size differentiation

Using tree height as a size variable, mean size differentia-

tion (TH) did not differ substantially among treatments (Fig. 8). Treatments producing uneven-aged structures, the unmanaged natural area and 5 year single-tree selection, had equal to slightly higher TH values than the commercial clear-cutting and fixed diameter-limit treatments, which were nearly always greater than those in the three-stage shelterwood. Harvest treatments did not produce large changes in TH, except following the commercial clear-cut treatment.

Although mean TH values did not differ among treatments, the frequency distribution of TH_i at each inventory did (Fig. 9). Both the unmanaged natural area and 5 year single-tree selection treatments had wide distributions of TH_i over time, with a large component of trees having $TH_i > 0.6$. Commercial clear-cutting, fixed-diameter limit harvesting, and the three-stage shelterwood treatments had few trees in these TH_i ranges. This observation suggested that there was more variation in height differentiation in local tree neighborhoods of uneven-aged stands than in irregular- or even-aged stands.

Structural complexity

The SCI produced unexpected results and did not reveal differences among treatments over time (Fig. 10a). Although SCI values for the unmanaged natural area and 5 year single-tree selection treatments were consistently high, SCI values for both the commercial clear-cutting and three-stage shelterwood treatments were equally high at certain stages in their development. The disparity among the natural area compartments also revealed a significant limitation to SCI. Compartment 32A was increasing in SCI, even though the stand was becoming much denser with only one to two canopy layers, while compartment 32B was declining in SCI, even though the stand was becoming less dense with multiple canopy layers.

Closer inspection revealed a correlation between SCI and tree density, thus limiting interpretations about changes in structural complexity. Simulations done by Saunders et al. (2002) suggested that SCI should be weighted by density^{- γ} , where γ ranged from 0.3 to 0.5 depending on spatial pattern and size range of the trees. Since trends among the treatments using γ equal to 0.3, 0.4, and 0.5 were not appreciably different, SCI was weighted with stem density^{-0.5} to produce a relative SCI (rSCI). The rSCI values were found to be consistently higher for the uneven-aged compartments (unmanaged natural area and 5 year single-tree selection) than for commercial clear-cutting, fixed-diameter limit, or three-stage shelterwood compartments (Fig. 10b). It was found, however, that rSCI could distort trends when tree densities were low ($n < 20$), as shown in the earliest inventories from the shelterwood compartments.

Summary of structural development

The final nonmetric multidimensional scaling (NMS) ordination of structural variables was significant ($p = 0.0196$), converging on a two-dimensional solution after 78 iterations and explaining 97.4% of the variation (Fig. 11). Final stress was 6.59 and final instability was 2.45×10^{-6} . Axis I of the ordination was positively associated with stem density, number of saplings, and the number of stems with $TH_i < 0.6$; these were generally collinear. Axis II of the ordination was

Fig. 6. Mean Clark–Evans nearest neighbor index (CE) for both saplings and trees (a) and only trees >11.4 cm DBH (b) for the unmanaged natural area and four silvicultural treatments by compartment from 1974 to 2002. Error bars represent ± 2 bootstrapped SE. Arrows denote harvest entries for each compartment. Values of CE < 1 indicate aggregation among tree stems and values of CE > 1 indicate regularity.

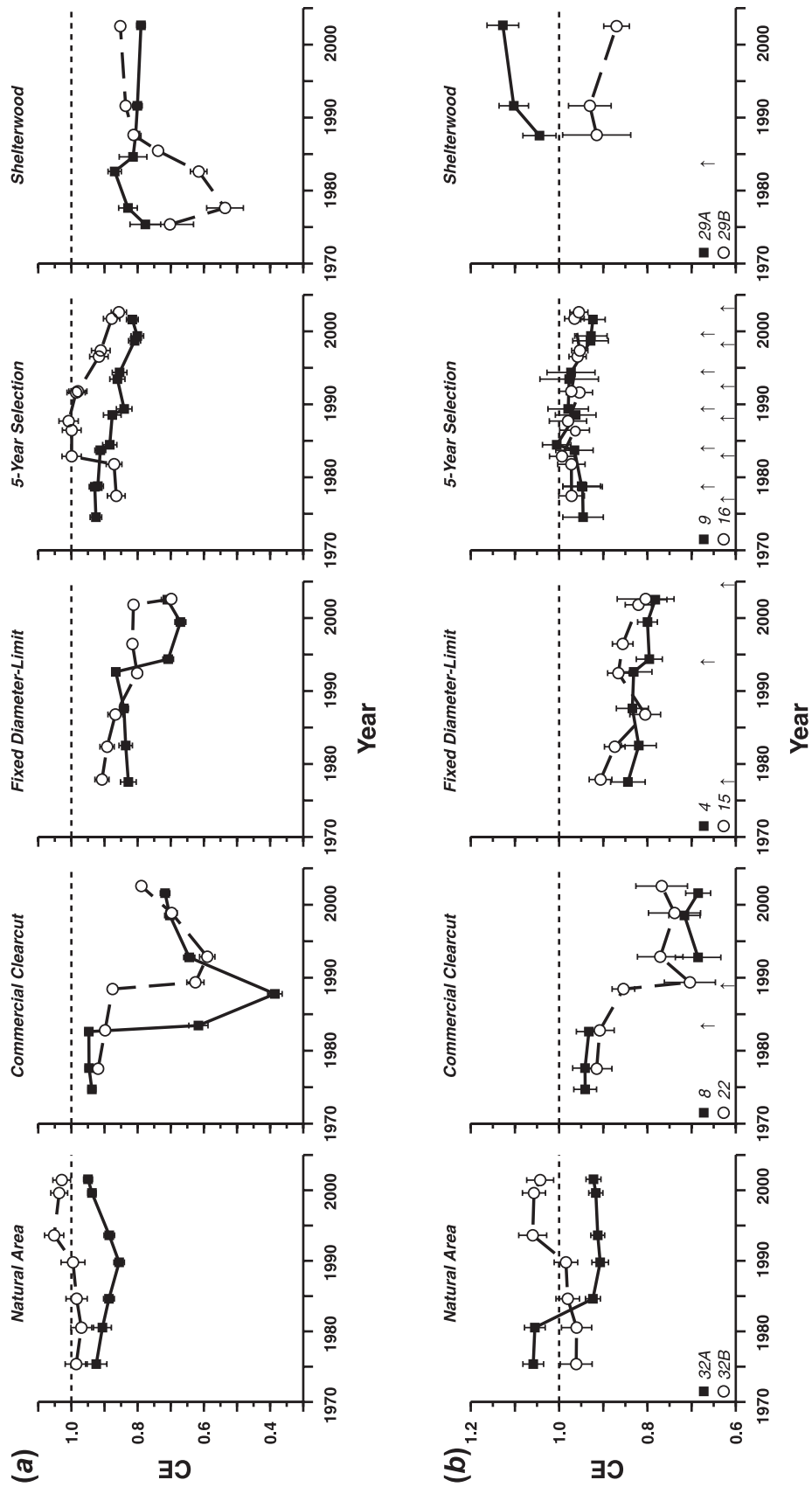
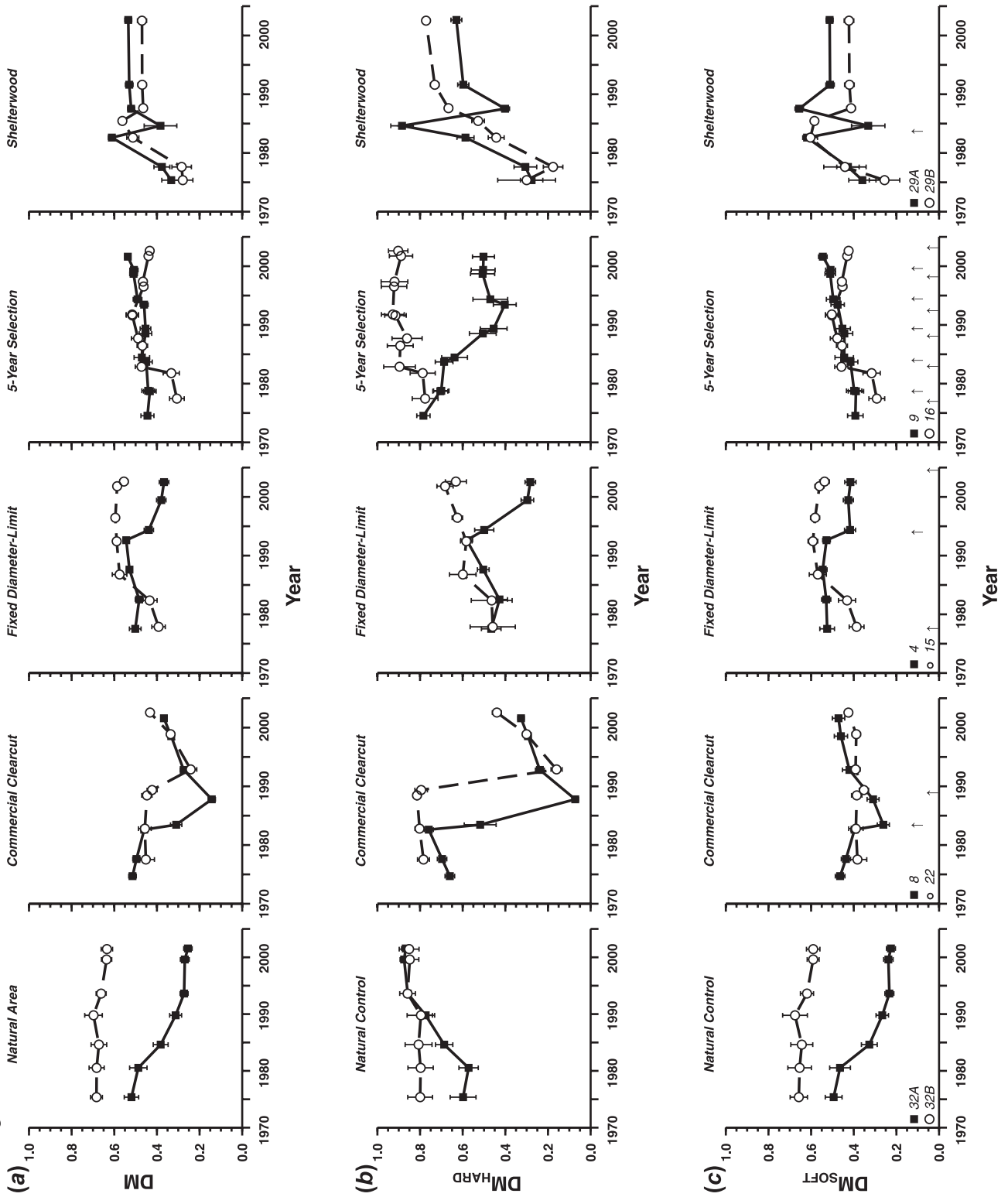


Fig. 7. Mean species mingling index (DM) for all stems (a), hardwood stems only (b), and softwood stems only (c) for the unmanaged natural area and four silvicultural treatments by compartment from 1974 to 2002. Error bars represent ± 2 bootstrapped SE. Arrows denote harvest entries for each compartment. DM values range from 0 (no intermixing of species) to 1 (perfect intermixing).



most strongly associated with hardwood importance (positively) and the number of sawlog-sized stems (negatively). Surprisingly, mean CE, TH, and DM had relatively minor effects on ordination scores along any axis (Fig. 11).

The NMS ordination exhibited a clear separation among uneven-, irregular-, and even-aged compartments, primarily along axis II (Fig. 11). The two natural area compartments showed a clear divergence within the NMS and were progressing into two different ordination spaces. The two 5 year selection compartments were notably static in ordination space, generally located between the two natural area compartments; harvests in these compartments had only minor effects on ordination scores. On the other hand, harvests in the fixed-diameter limit, commercial clearcut, and the three-stage shelterwood (with precommercial thinning) strongly affected ordination scores, generally moving the stands upwards and to the left in ordination space, likely reflecting the increasing importance of hardwoods and decreasing stem density. Further, since the harvests created younger stands, the fixed-diameter, commercial clear-cut, and three-stage shelterwood compartments changed most rapidly in ordination space over time.

Discussion

Influence of harvesting on development of stand structure

As we hypothesized, spatial aggregation was generally greater, and species mingling was generally lower with even-aged management or exploitative harvesting than with uneven-aged management or for unmanaged conditions (Figs. 6 and 7). These differences were likely driven by regeneration events that either occurred naturally (as in compartment 32A) or were induced by harvesting. This observation agrees with Phillips and MacMahon (1981), Skarpe (1991), Harrod et al. (1999), and Montes et al. (2005), who also reported increased aggregation from regeneration. Within the Acadian ecoregion, natural regeneration of trees is prolific, ranging from 25 000 to 80 000 trees·ha⁻¹, across a wide array of intensities and frequencies of partial overstory harvests (Brissette 1996). Balsam fir, in particular, can dominate the seed rain contribution in these stand types (Westveld 1931; Greenwood et al. 2003), and its early dominance tended to progressively reduce species mingling after regeneration events. Further, several northern hardwood species employed either a root-suckering or stump-sprouting regeneration strategy that caused strong aggregation at short scales (<2 m; Saunders 2006) and a large decrease in mingling, as the single-stemmed canopy tree would be replaced by multiple sprouts. We clearly saw this pattern following commercial clear-cutting and fixed diameter-limit harvests that shifted species composition towards hardwood dominance (Fig. 7).

We also confirmed our hypotheses regarding size (height) differentiation and structural complexity. Both differentiation (as measured by TH) and complexity (as measured by rSCI) were highest in multiple-strata, uneven-aged unmanaged natural area and 5 year selection treatments, intermediate in the irregularly aged exploitative harvests, and lowest with the even-aged, three-stage shelterwood treatment. These results were largely a function of tree size distribution

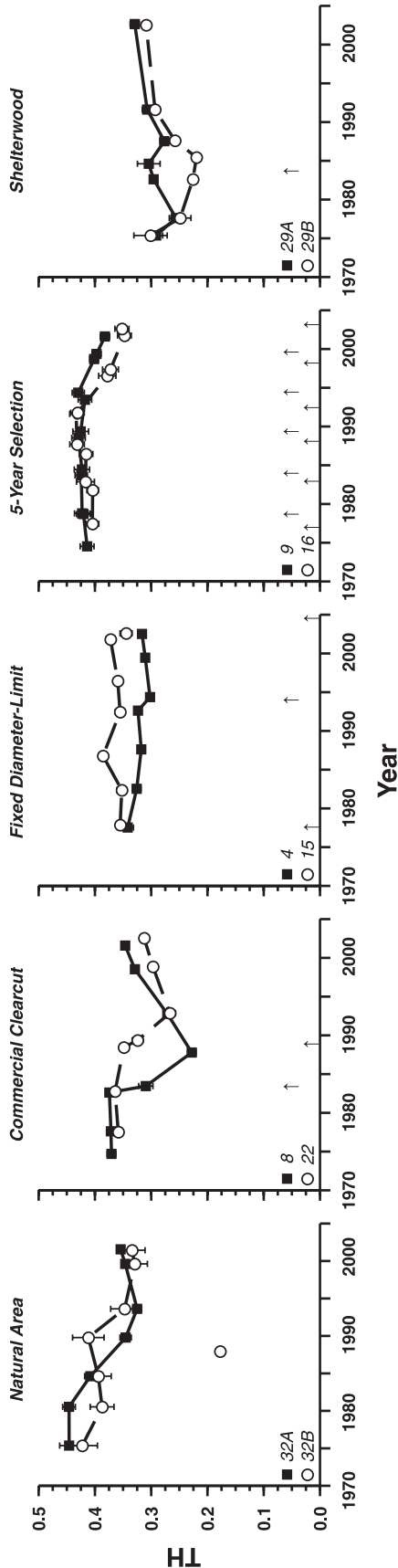
within each compartment, and not necessarily a valid comparison, as each treatment is at a different point in stand development. However, the distribution of TH_i values (Fig. 9) suggested that it will likely take several decades before the commercial clear-cutting and three-stage shelterwood treated stands approach the differentiation levels in 5 year selection or unmanaged natural area.

Although unreplicated in this study, the effect of PCT had mixed effects on structural development. The PCT increased height differentiation and structural complexity (Figs. 9 and 10), agreeing with the findings of Homyack et al. (2004), who reported that PCT increased canopy stratification and vertical height diversity by 11 years after thinning. Surprisingly, our study found that PCT increased species mingling primarily by increasing the species diversity of the stand (Figs. 4 and 7a). Growing space created by PCT appeared to allow a larger component of hardwood sprouts to survive rather than be outcompeted by neighboring softwoods (Lindgren and Sullivan 2001; Daggett 2003). Aggregation in the spatial pattern after PCT also increased as a function of the initially higher hardwood component, but aggregation has declined as hardwood sprouts have been outcompeted by the more uniformly spaced conifers (Saunders 2006).

The structural divergence between the two unmanaged natural area compartments may represent two distinct developmental pathways for these forest types (Fig. 11). Poor soil drainage in compartment 32A (Kenefic et al. 2005b) likely favored balsam fir over hemlock, and removal of overstory balsam fir by spruce budworm in the early 1970s caused that stand to prolifically regenerate to balsam fir, thus becoming much more aggregated (Fig. 6), unmingled (Fig. 7), and less differentiated (Figs. 8 and 9) over time. The structure of the stand is now more characteristic of an irregular, two-aged stand. In contrast, compartment 32B had a much higher proportion of hemlock in the overstory and subsequently did not experience a regeneration event. Structurally, the stand has been relatively stable in spatial pattern and mingling (Figs. 6 and 7), but is becoming slightly less differentiated (Fig. 9), as lower strata individuals slowly fall out of the stand. This late-successional stand will likely follow this trajectory until either some density-independent mortality event creates openings in the canopy and (or) hemlock eventually (over several decades) outcompetes other less shade-tolerant species. These two structural pathways would likely occur in an undisturbed Acadian forest landscape, as the proportion of balsam fir and hemlock often drive the dynamics in softwood-dominated stands (Seymour 1992).

Lastly, our results suggested that only the 5 year selection treatment would fall within the natural range of variability in spatial structure of the two natural area compartments (Fig. 11). Uniform shelterwood, as was applied in this study, created an undifferentiated and less complex structure that differed from the natural stands, although over time these stands may approach the structural attributes of the natural stands, as competition reduces stem densities and size differentiation increases with tree growth. Following multiple harvest entries, the commercial clear-cutting and diameter-limit treatments created a more aggregated and less complex structure than natural development. However, we hypothesize that these stands would take much longer to approach

Fig. 8. Mean height differentiation index (TH) for the unmanaged natural area and four silvicultural treatments by compartment from 1974 to 2002. Error bars represent ± 2 bootstrapped SE. Arrows denote harvest entries for each compartment. A TH of 0 indicates that all trees in the stand were the same height.



the structural attributes of the natural stands than the shelterwood treatments, primarily because of a shift in composition towards early successional, sprouting hardwood species.

Adequacy of the stand complexity index

We found the SCI in its original form to be biased when comparing stands of vastly different structures and densities. For the few applications of SCI found in the literature (e.g., Zenner and Hibbs 2000; Zenner 2004), the stands that were compared had stem densities that varied by only a factor of two to three, were all of the same general forest type and composition, and represented a chronosequence along the same development pathway. In this study, stem densities varied by 45-fold across compartments and inventories, were of vastly different forest types and compositions, and were not on the same development pathways. Although one could argue that the inherent bias in SCI has been inflated in this study, since it was calculated on all measured tree stems (e.g., Zenner and Hibbs (2000) used a 5 cm DBH lower threshold), small diameter stems make up a significant component of the structure in many early-successional stands, and several of these stands would have no SCI value until far into stem exclusion. Use of the rSCI provided an improvement, as it removed the influence of density on SCI, making the index more responsive to size differentiation and spatial pattern.

Regardless of its form, SCI also can be criticized in that it does not explicitly recognize that canopy gaps increase structural complexity (McElhinny et al. 2005). With large-scale plots, this weakness can be overcome using a “moving-window” approach and quantifying the distribution of local SCI values within a stand (Zenner 2005). Canopy gaps would then occur in locations where SCI was extremely low compared with neighboring windows. This approach would approximate the distribution of TH_i , where the number of neighbors included in each estimate of TH_i increased with the size of the window. The TH_i does not necessarily require a complete enumeration of all tree locations and sizes in a stand (von Gadow and Hui 1999), and therefore, might be more practical than SCI for many applications. Further, the distribution of TH_i values within a stand may have higher discriminatory power than rSCI alone (Fig. 11).

Effectiveness of spatial model

Overall, results from the structural model developed in this study generally agreed with earlier studies of this experiment by Brissette (1996), Sendak et al. (2003), and Kenefic et al. (2005a). These earlier works had focused on conventional changes in basal area and diameter distributions, and species composition to investigate the ecological and financial viability of the various management systems. Their combined results suggested that there were structural differences among treatments, but low replication often limited the power of formal statistical comparisons. In contrast, this study took a Monte Carlo based approach that incorporated variability at the plot level, thereby detecting substantial differences among treatments for most spatially explicit structural metrics.

However, we were disappointed at the marginal information gains achieved in this study given the high computa-

Fig. 9. Frequency distribution of the height differentiation index value for individual tree stems (TH_i) in the unmanaged natural area and four silvicultural treatments by compartment from 1974 to 2002. Higher values indicate neighborhoods with greater vertical diversity.

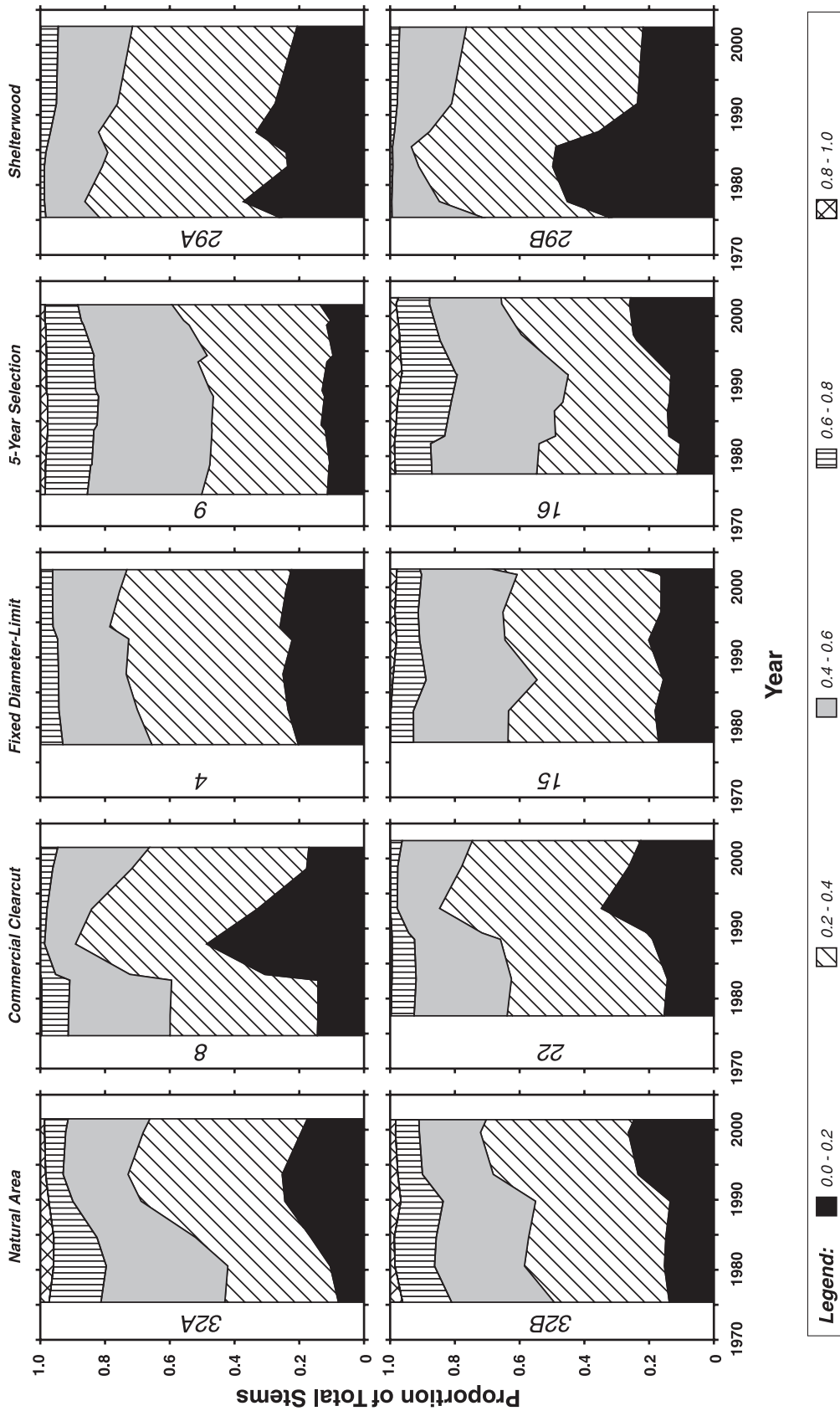


Fig. 10. Mean absolute (a) and relative (b) stand complexity index (SCI) for the unmanaged natural area and four silvicultural treatments by compartment from 1974 to 2002. Error bars represent ± 2 bootstrapped SE. Arrows denote harvest entries for each compartment. SCI ranges upwards from 0, which occurs only when all tree stems are the same height.

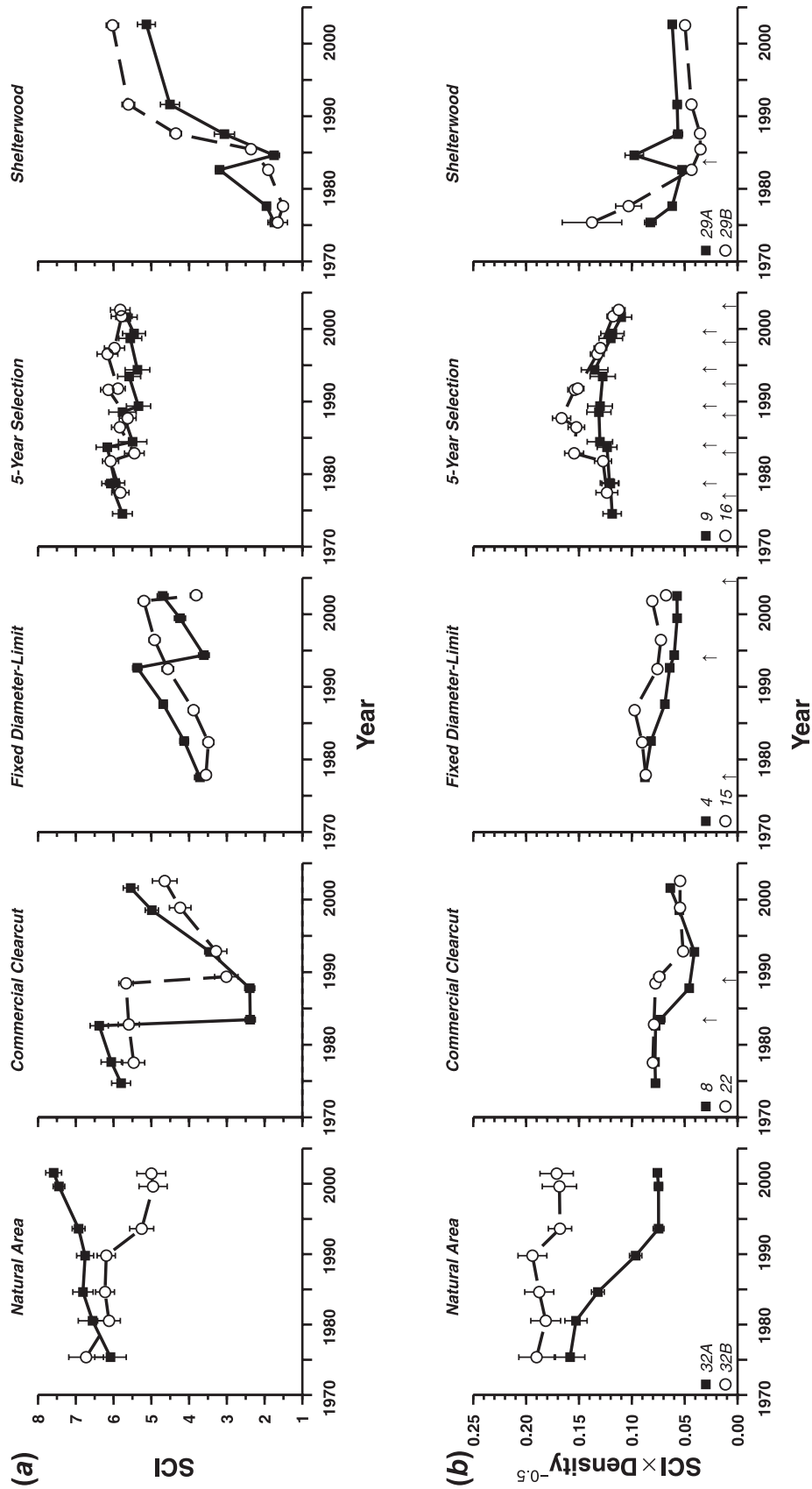
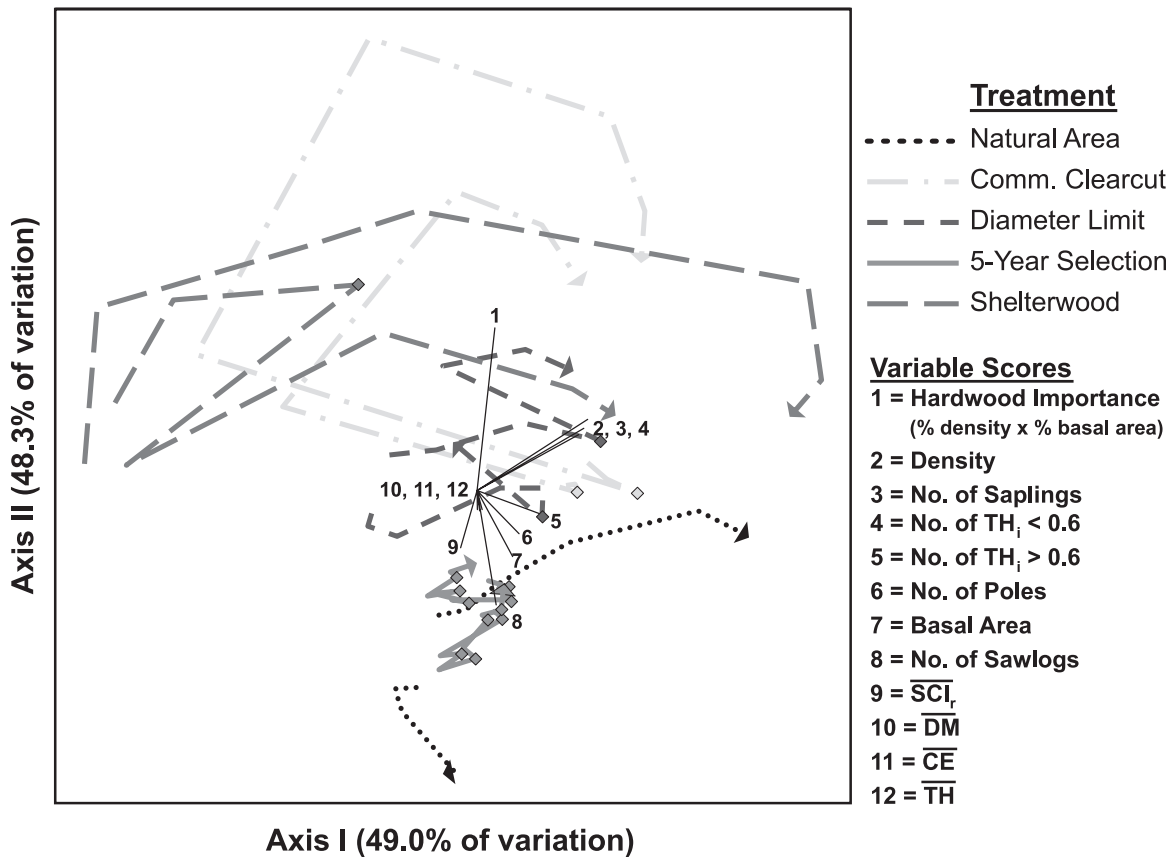


Fig. 11. Nonmetric multidimensional scaling (NMS) ordination of spatial and nonspatial structural variables for the compartments for 1974–2002 by treatment. Harvest entries are indicated by diamonds. Variable scores are plotted from the centroid of the data and represent both the strength and direction of “pull” of that variable in the ordination.



tional costs of the spatial indices. Plot-level means of CE, DM, and TH were not very useful, although the distribution of values for those indexes (e.g., DM_i or TH_i) across subpopulations were quite useful. We feel that both the prolific natural regeneration in the stands and the averaging of compartment-level spatial relationships across realizations of plots muted potential differences that would have been detected more clearly by these indices.

Our structural model also had some weaknesses that were not immediately apparent. For compartments with low tree relocation rates (Table 1), the random placement of unknown stem locations within the model likely caused an underprediction of aggregation, an overprediction of mingling, and some bias within size differentiation patterns, that together weakened the discriminatory power of the spatial indices (Fig. 11). These biases were generally greatest in the earlier inventories (before 1990), since fewer dead stems were relocated. Further, Saunders (2006) noted that the morphing algorithm introduced some bias into plot estimates of spatial pattern, particularly for plots that were extremes within any particular compartment. However, the morphing algorithm should not appreciably change the mingling or size differentiation patterns, as most local spatial relationships would not change except when subplots abutted one another. Obviously, overlay of the scaled sapling subplot onto the tree plot would change some spatial characteristics, but since saplings dominated the spatial pattern in most compartments, this bias should be minimal.

This structural model was designed to take advantage of spatially explicit, longitudinal measurements on small-scale (<0.1 ha), forest inventory plots. Generally, spatial analyses of these types of inventory plots have generally been avoided because of a lack of spatial inference from the small plot size and difficulties in scaling patterns of subpopulations from nested plot designs. Instead, most researchers have relied on a few (five or less) large plots that map spatial relationships among only the largest size-classes. This approach has power in that larger scaled patterns can be detected and edge influences on pattern are minimized. However, there are few studies of repeatedly measured, large-scale plots. Ward et al. (1996) provide a rare example where the spatial dynamics of an old-growth deciduous forest were characterized across three inventories spanning a total of 60 years. Thus, for most studies, there is a trade-off between spatial and temporal scale. Our spatial models took advantage of the temporal scale.

Spatial analysis of forest inventory plots offers additional benefits over traditional analysis of larger plots. Forest inventories can be designed to more efficiently and economically capture the mean and range of neighborhood conditions within a stand than one large plot of the same total sampled area. Therefore, plots can be randomly located within stands or strata, rather than biasedly placed to capture the range of spatial relationships found in the stand. Multiple plots also allow spatial inference to be drawn from the experimental design rather than comparisons with stochastic

models (i.e., csr) that must be assumed for individual plots (Diggle 2003). Lastly, at adequate sample intensities, broader scale spatial analyses beyond the scale of an individual plot can still be conducted using the sample plot means for any spatial indices of interest (Fúle and Covington 1998).

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