Changes to preindustrial forest tree composition in central and northeastern Ontario, Canada

F. Pinto, S. Romaniuk, and M. Ferguson

Abstract: Preindustrial forest composition for >180 000 km^2 throughout central and northeastern Ontario was recreated from Ontario Crown land survey notes (1816–1955) and compared with existing forest composition derived from current Forest Resource Inventories (1998–2009) in each of Site Regions 3E, 4E, and 5E. A validation analysis was performed using the Forest Resource Inventory data to test the assumption that sampling the land survey tree species composition along township boundaries is adequate in describing the composition of the whole forest. The majority of tree species in each of the three site regions validated successfully. A binary logistic regression model allowed birch genera to be classified at the species level to aid in the interpretation of survey notes. All analyses showed significant reductions in conifers (especially red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and eastern larch (*Larix laricina* (Du Roi) K. Koch)) and significant increases in maple (*Acer* spp.), oak (*Quercus* spp.), white birch (*Betula papyrifera* Marsh.), and poplar (*Populus* spp.).

Résumé : La composition forestière préindustrielle d'une aire de plus de 180 000 km^2 dans le centre et le nord-est de l'Ontario a été reconstituée à partir de notes d'inventaire des terres publiques de l'Ontario (1816–1955) et comparée à la composition forestière actuelle déterminée à partir des inventaires des ressources forestières (1998–2009) dans chacune des régions écologiques 3E, 4E et 5E. Une analyse de validation a été effectuée avec des données de l'inventaire des ressources forestières pour tester l'hypothèse que l'échantillonnage de la composition forestière de l'inventaire des terres le long des limites de comté est adéquat pour décrire la composition de l'ensemble de la forêt. La majorité des espèces d'arbre dans chacune des trois régions écologiques ont été validés avec succès. Un modèle de régression logistique binaire a permis de classifier les bouleaux à l'espèce pour faciliter l'interprétation des notes d'inventaire. Toutes les analyses ont montré qu'il y avait une réduction significative des conifères (en particulier le pin rouge (*Pinus resinosa* Ait.), le pin blanc (*Pinus strobus* L.) et le mélèze laricin (*Larix laricina* (Du Roi) K. Koch)) et une augmentation significative des érables (*Acer* spp.), des chênes (*Quercus* spp.), du bouleau à papier (*Betula papyrifera* Marsh.) et des peupliers (*Populus* spp.).

[Traduit par la Rédaction]

Introduction

Preindustrial forests (also referred to as presettlement forests) are those forests that existed just before or during the early stages of their industrial use (Frelich 1995; Dyer 2001). Preindustrial forest information serves an important role in improving the understanding of natural forest patterns and processes to aid in the management of forestry activity. To compare and develop strategies for implementing ecosystem management, preindustrial forests also provide a template for conservation and restoration of forest biodiversity by revealing the processes by which the forests were established. Forest managers that seek to work toward a desired future forest composition often require a preindustrial forest description to meet regulatory requirements for some jurisdictions such as Ontario (OMNR 2004) and certification systems such as the Forest Stewardship Certification system (FSC Canada Working Group 2004). Preindustrial forest descriptions have also been used to improve our understanding of forest disturbance regimes (Canham and Loucks 1984; Whitney 1986; Zhang et al. 1999), the effects of climate change (Davis 1981; Campbell and McAndrews 1993; Russell et al. 1993), forest age structure (Prentice 1986; Frelich 1995; Lorimer 2001), and tree community associations with landform (White and Mladenoff 1994; Black and Abrams 2001).

The Ontario Crown land survey (OLS) data from early township surveys contain geographically referenced forest stand descriptions along a survey line and witness trees at the intersection of boundaries. Unlike the public General Land Office surveys in the United States, the density of witness trees recorded in most of Ontario is quite low. In most of central and northeastern Ontario, the OLS usually recorded witness trees only at the corners of each township, limiting their use to describe past forest conditions. However, the methods used and transect descriptions by early land surveyors to collect and record their data in Ontario have generally been consistent (Canada Department of Crown Lands 1862, 1867; Gentilecore and Donkin 1973*a*, 1973*b*). This makes OLS data suitable for recreating forest conditions prior to widespread human use and settlement. Certain biases and errors associated with the land survey information have been suggested (Noss 1985; Simard and Bouchard 1996). The limitations in land surveys are primarily related to the coarse resolution of the data (He et al. 2007) and the selection of witness trees, which tend to be

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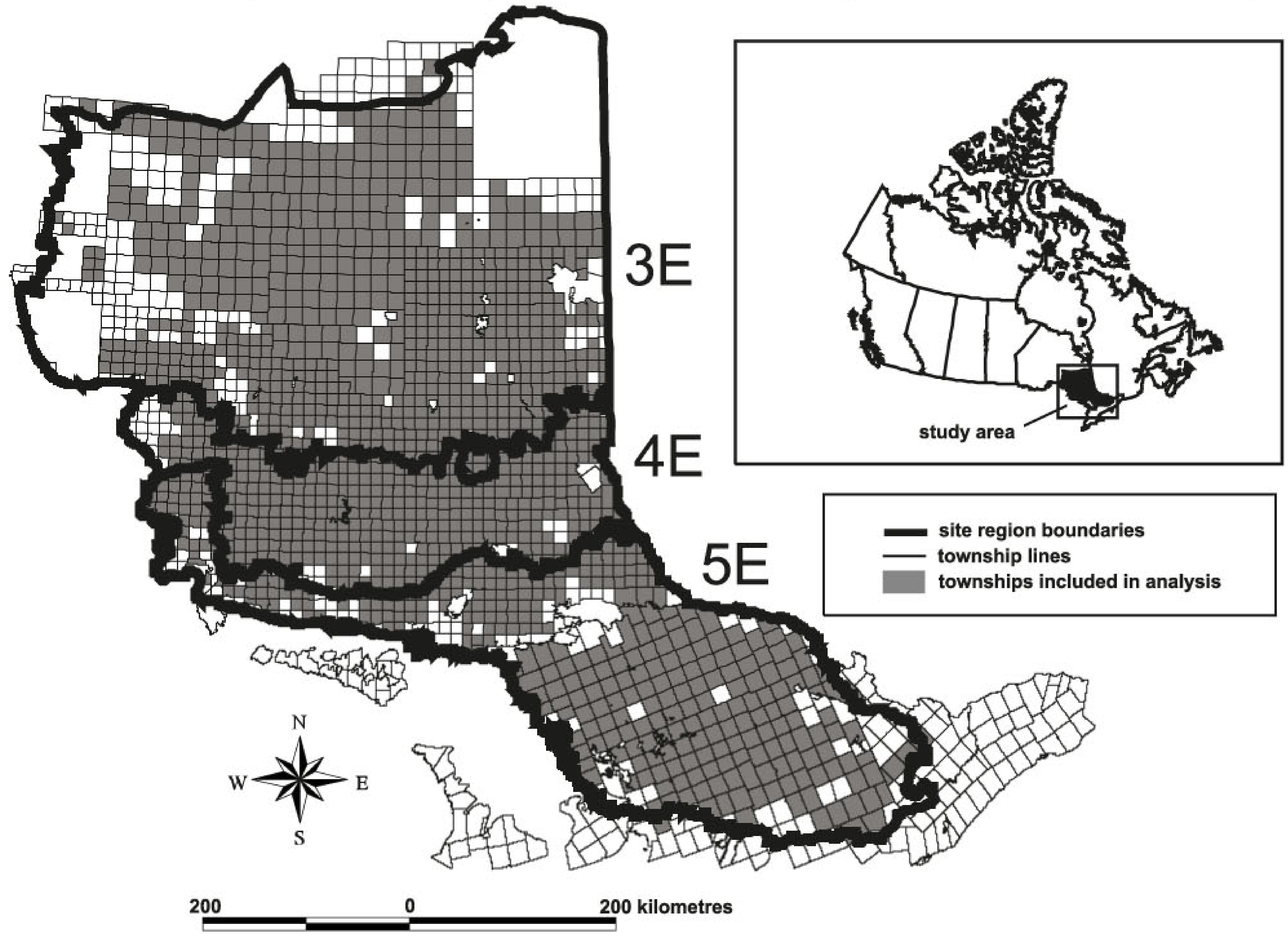
Fig. 1. Outline of the township boundaries in the study area that includes the three site regions in central and northeastern Ontario, Canada.



long-lived trees, and the tendency to overrecord the presence of commercially important tree species along transects (White 1984; Galatowitsch 1990; Schulte and Mladenoff 2001).

Land survey data have been used to describe preindustrial forests in the northeastern United States (e.g., Radeloff et al.1999; Dyer 2001; He et al. 2007; Manies and Mladenoff 2000) and more recently in Ontario and Quebec in Canada (e.g., Clarke and Finnegan 1984; Simard and Bouchard 1996; Jackson et al. 2000; Leadbitter et al. 2002; Pinto and Romaniuk 2003; Suffling et al. 2003). These studies all cover small portions of large ecological zones. This limits the utility of their results to provide information on or enable decision making over a large area. Schulte and Mladenoff (2001) and Wang and Larsen (2006) suggest providing a description of the preindustrial forest composition over a large spatial (regional) scale. These studies have the advantage of incorporating greater environmental heterogeneity and the ability to reconstruct landscape spatial patterns of individual species. Further, Wang and Larsen (2006) suggest coarsely resolved spatial data on a 6 mile × 6 mile (10 km × 10 km) grid (township scale) is more visually and statistically stable when large areas are analyzed.

The objectives of our study are to (*i*) determine if sampling along survey boundaries is adequate to describe the composition of the whole forest and (*ii*) describe the changes in dominance and importance value of tree species that grew at the time of the preindustrial land survey and stands growing today at a large regional scale.

Materials and methods

Study area

Our study area encompasses >180 000 km^2 of central and northeastern Ontario, Canada (Fig. 1). This large area covers portions of both the Great Lakes – St. Lawrence (GLSL) forest region and the boreal forest region (Rowe 1972). For analyses, we separated the data into Site Regions (SR) 3E, 4E, and 5E described by Hills (1959). SR3E) corresponds well to the boreal forest region and is characterized today by black (*Picea mariana* (Mill.) BSP) and white spruce (*Picea glauca* (Moench) Voss) with jack pine (*Pinus banksiana* Lamb.) and balsam fir (*Abies balsamea* (L.) Mill.) and hardwoods, such as white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and balsam poplar (*Populus balsamifera* L.). Similarly, SR5E corresponds to the GLSL forest region, which today contains a mix of tree species characterized by white (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) , eastern hemlock (*Tsuga canadensis* (L.) Carr.), yellow birch (*Betula alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and northern red oak (*Quercus rubra* L.). SR4E represents the GLSL forest region dominated by conifers such as white pine, spruces, and hardwoods such as poplar, white birch, and smaller amounts of yellow birch and maples.

Preindustrial forest cover

The preindustrial forest composition was reconstructed for each SR in the study area using OLS notes from 1816 to 1955. Over 99% of the surveys were conducted between 1854 and 1931 and collected by 172 different survey parties. More recent survey dates do not necessarily mean that they were more likely to be logged or cleared at the time of the survey; northern townships were generally surveyed later, but they were also cleared or settled later.

The OLS contain spatial information as well as a description of the tree cover along the boundaries of each township, the location and extent of forest stands along these boundaries, and a list of the tree species and genera present within each stand. Stands were delineated based on the changes in composition (proportion accounted for by each taxon) or changes in the order in which tree species were listed. Records of instructions given to Ontario land surveyors in the past suggest that tree species in a stand had to be listed in order of their abundance (Canada Department of Crown Lands 1862, 1867; Gentilecore and Donkin 1973*a* , 1973*b*). The data in our study included only observations along the township boundaries and excluded data from lot and concession lines within the townships, because full township surveys were not consistently completed across Ontario.

Current forest cover

The forest resource inventory (FRI) data that describe the current species composition of the study area are based on the interpretation of aerial photographs updated with harvesting forecasts, depletions, and regeneration. The inventory is composed of polygons that delineate individual forest stands. One limitation of using FRI data are that changes in composition of understory and (or) small-crowned species (e.g., eastern white cedar (*Thuja occidentalis* L.) and balsam fir) may arise not from an actual change but from differences between the ground-based OLS and the aerial photographs used to create the current FRI. A second limitation is that, in Ontario, photointerpreted FRI before 2007 was not validated through ground sampling. Potvin et al. (1999) and Pinto et al. (2007) show that errors in describing tree species composition through photointerpretation do happen and result in errors in describing the current composition of a forest. To reduce errors that may occur with tree growth, reproduction, and mortality, the most current inventory data available were used in our analyses, i.e., >70% of our study area was updated between 2001 and 2006.

Comparison of FRI data along the township boundary to the abundance of tree species described by the FRI data within the whole township

To determine whether species abundance along the boundary of a township adequately predicted the abundance of tree species within the whole township, we transcribed the FRI along the township boundary lines and compared the results with the FRI for the whole township. The strength of the similarity determines the validity of using the OLS, which only describes forest composition along the township boundary, to estimate the species composition of entire townships, and thus, the validity of comparing the OLS data with the current FRI data as a means of examining postindustrial changes.

Townships from each SR were selected for analysis based on two criteria: (*i*) townships that had OLS data for ≥95% of the township perimeter and (*ii*) townships that had FRI data for ≥95% of the township area. (Small islands within lakes along township boundaries were not included, because forest data were not listed for these areas in the OLS.) The data from the FRI were mapped to the level of individual townships using Arcview 3.2 GIS software (Environmental Systems Research Institute, Inc. 1996), and the area of forested polygons was used to calculate the percentage composition of the first-listed species; this is the dominant species and, in most cases, the working-group species for the township. The resulting data set represented the percent composition for the whole township. We ran an intersect operation in Arcview to retrieve the stand descriptions from the FRI along township boundaries using the OLS transects as a reference. This let us establish a correspondence between the FRI and OLS data. We then compared these intersected boundaries with the percent composition for the whole township to determine how accurately the boundary descriptions described the overall forest of the township. We used the Wilcoxon's signed ranks test (SPSS Inc. 2002) for nonnormal samples and a paired *t* test for normally distributed samples (with or without arcsine square root transformations) to compare the species compositions of each of the 501, 310, and 234 townships in SR3E, SR4E, and SR5E, respectively. We performed a retrospective power analysis using PASS (Hintze 2000) to quantify the effect size of our data sets using a high power (0.80, β = 0.20) and an alpha level of 0.05. We calculated an effect size based on a fixed power, because Steidl et al. (1996) cautioned that using the observed effect size from the study is incorrect and misleading. In addition, Rotenberry and Wiens (1985) advocated focusing attention on the effect size of a phenomenon rather than β. Only the boundary lines from the above townships were included in the OLS and FRI comparisons described below. Most townships were either 6 miles × 6 miles (10 km × 10 km) or 9 miles × 9 miles (14.5 km × 14.5 km); other shapes and sizes occurred, especially in the southern portion of the study area.

Comparison of species abundance between OLS and FRI data

Current (FRI) and preindustrial (OLS) data were compared along each township boundary using individual boundaries as the sampling unit. Analyses were performed at two levels. The first comparison summarized the proportion of township boundary occupied by the first-listed species (hereafter dominant species) in each stand.

The second comparison calculated an importance value called the "ranked abundance" for both data sets. The ranked abundance represents the length of the boundary occupied by each species but weighted based on the rank of the species (i.e., the order in which it was listed) in a stand; the first species was given a weighting of three times its actual length, versus two times for the second species and once for the third and subsequent species. This ranking was used to test the assumption that the species were listed in

Table 1. Common and scientific names associated with the names and codes used in the OLS.

Survey notes	Interpretation	Scientific name
Unspecified ash	Ash species (A)	*Fraxinus* spp.
Black ash	Black ash (AB)	*Fraxinus nigra* Marsh.
White ash	White ash (AW)	*Fraxinus americana* L.
Alder	Alder species (AL)	*Alnus* spp.
Beech	American beech (BE)	*Fagus grandifolia* Ehrh.
Balsam	Balsam fir (BF)	*Abies balsamea* (L.) Mill.
Unspecified birch or bouleau	Birch species (BIR) or bouleau (BL)	*Betula* spp.
Paper birch or white birch	White birch (BW)	*Betula papyrifera* Marsh.
Yellow birch or black birch	Yellow birch (BY)	*Betula alleghaniensis* Britt.
Cedar	Eastern white cedar (CE)	*Thuja occidentalis* L.
Hemlock	Eastern hemlock (HE)	*Tsuga canadensis* (L.) Carr.
Tamarack	Tamarack or larch (LA)	*Larix laricina* (Du Roi) K. Koch
Unspecified maple	Maple species (M)	*Acer* spp.
Hard maple	Sugar maple (MH)	*Acer saccharum* Marsh.
Soft maple	Red or silver maple (MS)	*Acer rubrum* L. or *Acer saccharinum* L.
Unspecified aak	Oak species (O)	*Quercus* spp.
Black oak	Black oak (OB)	*Quercus velutina* Lamb.
Red oak	Northern red oak (OR)	*Quercus rubrum* L.
White oak	White oak (OW)	*Quercus alba* L.
Banksian, pitch, or jack pine	Jack pine (PJ)	*Pinus banksiana* Lamb.
Poplar	Poplar species (PO)	*Populus* spp.
Unspecified pine	Pine species (P), excl. *P. banksiana*	*Pinus* spp.
Red, Norway, or yellow pine	Red pine (PR)	*Pinus resinosa* Ait.
White pine	White pine (PW)	*Pinus strobus* L.
Unspecified spruce	Spruce species (SP)	*Picea* spp.
Black spruce	Black spruce (SB)	*Picea mariana* (Mill.) BSP
Red spruce	Red spruce (SR)	*Picea rubens* Sarg.
White spruce	White spruce (SW)	*Picea glauca* (Moench) Voss
Unspecified hardwood	Hardwood (H)	
Mixed timber	Unknown species mixture (MT)	
All ash categories listed above	Ash species (A, AW, AB)	*Fraxinus* spp.
All birch categories listed above	Birch species (BIR, BL, BW, BY)	*Betula* spp.
All maple categories listed above	Maple species (M, MH, MS)	*Acer* spp.
All oak categories listed above	Oak species (O, OB, OR, OW)	*Quercus* spp.
All pine categories listed above	Pine species (P, PR, PW)	*Pinus* spp.
All spruce categories listed above	Spruce species (SP, SB, SR, SW)	*Picea* spp.

Note: The last six rows represent the groupings that we used in our analyses.

order of abundance. We also calculated an importance value called "equal abundance" for all species using the actual (unweighted) length of each forest stand along the boundaries in the study area. We used the ranked and equal importance values to calculate the percent composition of each boundary being compared. Each value is expressed as the percent length of each species and represents the mean for all township boundary lines. We used the Wilcoxon's signed ranks test (SPSS Inc. 2002) for non-normal samples and a paired t test for normal samples (with or without arcsine square root transformations) to compare the species proportions of each of the 1218, 678, and 589 different township boundaries in SR3E, SR4E, and SR5E, respectively. Boundaries that were less than 1000 m in length were excluded from the analyses. We used PASS (Hintze 2000) to test the power of these dominant species data sets using the same criteria outlined in the above power analysis.

The surveyors often described only the genus of the trees observed along the township boundaries; this was the case for ash (*Fraxinus* spp.), birch, maple, oak, pine, and spruce. For example, different surveyors described the birch genus as birch, bouleau (French for "birch"), white birch, paper birch, yellow birch, or black birch. The latter was assumed to be yellow birch, which appears darker in colour when it is older and, for this reason, has been commonly referred to as black birch (Erichsen-Brown 1979). When pine was mentioned in the historical data, we classified it as red pine and white pine; jack pine was always specified as jack pine, Banksian pine, or pitch pine and, thus, was not included in the "unspecified pine" or "pine species" groupings used in the analyses (Table 1). The unknown hardwood (H) category was often used by land surveyors; individual conifer species or genera were listed specifically when appearing in these hardwood stands greater than 95% of the time. No assumptions were made for the mixed timber category, because it could have included any mixture of species. Dominant species in the FRI and OLS data that accounted for <1% of the forest composition were excluded from the composition based analyses (Table 2).

We tried to separate individual species for stands in the

Table 2. Species that made up <1% of the total forest composition by dominant species.

		Data set		
Common name	Scientific name	SR3E	SR4E	SR5E
Balsam poplar	*Populus balsamifera* L.	OLS, FRI	OLS, FRI	OLS
Basswood	*Tilia americana* L.	—	—	OLS, FRI
Blue oak	Unknown (burr oak?)	—	—	OLS
Cherry	*Prunus* spp.	OLS	OLS	OLS, FRI
White elm	*Ulmus americana* L.	—	OLS	OLS, FRI
Hazel	*Corylus* spp.	OLS	OLS	OLS
Ironwood	*Ostrya virginiana* (Mill.) K. Koch	OLS	—	OLS, FRI
Moosewood	*Acer pensylvanicum* L.	OLS	—	—
Scots pine	*Pinus sylvestris* L.	—	FRI	FRI
Whitewood	Unknown	OLS	—	—
Willow	*Salix* spp.	OLS	OLS	OLS

OLS data that had been recorded ambiguously or only to genus (such as "bouleau" or "birch") into individual species through the development of a binary logistic regression model (SPSS 2002). The model was built using the differentiated OLS data (i.e., white birch and yellow birch) based on the presence or absence of tree species in all three SRs. We created a separate database for birch stands in the OLS data where white birch was given a value of 0 and yellow birch a value of 1. If both species appeared in a stand, the species with the higher ranking (i.e., the species closer to the beginning of the list of species in the survey data) was included, and the other species was excluded. In addition for each stand, the SR was also used as a variable in model development. The cutoff value used in the model was based on the frequency of the known birch species in the OLS data. If the model was significant (model χ^2; SPSS Inc. 2002) and showed >70% overall classification accuracy, then the species would be changed by running the model again but on the nondifferentiated OLS genera. Regardless of success of the model, the generic birch grouping was also maintained for nonassumption-based comparisons.

In the analysis of broad categories for the trees based on dominant species, the OLS and FRI data were regrouped into intolerant hardwoods (poplar; white birch; and cherry (*Prunus* spp.), midtolerant to tolerant hardwoods (ash; American beech (*Fagus grandifolia* Ehrh.), basswood (*Tilia americana* L.), ironwood (*Ostrya virginiana* (Mill.) K. Koch), oak, maple, and yellow birch), and conifers (balsam fir; eastern white cedar; hemlock; eastern larch (*Larix laricina* (Du Roi) K. Koch), pine; and spruce) and compared based on the proportion of a township boundary's total length occupied by each group. We used the Wilcoxon's signed ranks test to compare the groups of related proportions.

The OLS contains references of logging such as "removed for pulp," "partially lumbered," or "best timber removed." Other statements in the OLS indicate agricultural development. These references were used to determine the proportion of the study area that had been logged or cleared for farming before the OLS.

Limitations

Studies involving land survey notes usually select one to three surveyors in an area. The advantage is less variation in recording style. Landscape-scale studies will contain survey notes from several Ontario Crown Land surveyors and over an extensive timeframe; combining the data from a large number of surveyors is more likely to introduce differences with respect to tree species codes and comments. However, a majority of the OLS notes are dated after 1859, after the split-line method was in use, and the surveyor instructions were fairly standardized in what is now the province of Ontario (Clarke and Finnegan 1984). Comparably, there were greater than 20 versions of instructions for General Land Office Surveyors in the United States between 1804 and 1902 (Galatowitsch 1990).

Other problems attributed to land survey data include incomplete coverage (private land and remote areas), loss of data, possibility of fraudulent surveys (these were often resurveyed), and legibility of handwriting and microfiche copies (Hutchinson 1988; Galatowitsch 1990).

Results

Sampling tree species composition along the OLS township boundaries provided an acceptable measure of the overall composition for the majority of tree species in each of the three SRs in our study. That is, the forest cover recorded along the boundaries between townships predicted the overall forest composition with 95% confidence in most cases except for those species specified in Table 3, which were significantly different (α = 0.05). This means that sampling along the OLS township boundaries may be insufficient to detect changes in abundance for these species. Effect sizes ranged from 0.2% to 1.3% for the three SRs, from 0.6% to 1.3% for species compositions >10%, and from 0.2% to 0.9% for compositions between 1% and 10%. We had no power to detect differences for compositions <1% (effect sizes could not be calculated).

Changes in occurrence of tree species between the OLS and FRI data were detected for both common and less common species. The pine species group, i.e., red and white pine, decreased significantly in all three SRs, and maples and poplar increased significantly (Table 4). The "oak species" group has also increased significantly where it was analyzed. The H category in SR5E accounted for 8% of the forest composition in that SR; most hardwood species (beech and total maple) were significantly different without incorporating this additional H data; however, this may account for the low amount of oak species recorded in the

Table 3. Tree species composition of the FRI for SRs along township boundaries as compared with the total forest based on the dominant species.

	SR3E (1998–2006)			SR4E (1998–2004)			SR5E (1998–2009)		
Species or species group	Township lines	Total forest	p (α = 0.05)	Township lines	Total forest	p (α = 0.05)	Township lines	Total forest	p (α = 0.05)
AB	0.01	0.01	0.396*	0.01	0.02	0.287*	0.58	0.59	0.430*
AW	np	np		np	np		0.02	0.02	0.062*
Ash species	0.01	0.01	0.396*	0.01	0.02	0.287*	0.60	0.61	0.469*
BE	np	np		np	<0.01	0.317*	0.02	0.27	0.094*
BF	2.67	2.88	0.918*	2.38	2.29	0.782*	5.28	5.76	0.065*
BW	10.54	8.94	0.184*	26.38	25.95	0.874†	9.48	7.40	0.122*
BY	0.08	0.06	0.724*	1.27	1.17	0.234*	3.28	2.66	0.940*
Birch species	10.62	9.00	0.197*	27.65	27.12	0.986†	12.76	10.07	0.189*
CE	2.07	2.15	0.012*	2.53	2.78*	<0.001*	3.02	3.25	0.065*
HE	np	np		0.01	0.02	0.715*	2.34	2.91	0.336*
LA	1.23	1.36	0.184*	0.11	0.12	0.145*	0.24	0.28	<0.001*
MH	0.07	0.05	0.506*	4.96	4.41	0.004*	34.23	36.92	0.349*
MS	0.05	0.03	0.475*	0.79	1.08	<0.001*	4.31	4.73	0.357*
Maple species	0.13	0.08	0.365*	5.74	5.49	0.919*	38.55	41.65	0.465*
OR	np	np		0.14	0.16	0.249*	3.30	3.76	0.297*
OW	np	np		np	np		0.03	0.02	0.327*
Oak species	np	np		0.14	0.16	0.249*	3.32	3.78	0.342*
PJ	11.09	10.29	0.850*	21.55	22.35	0.654*	2.17	1.69	0.770*
PO	19.75	20.62	0.297†	14.23	14.88	0.956*	16.75	15.77	0.056*
PR	0.01	0.01	0.705*	1.20	1.15	0.597*	1.53	1.58	0.065*
PW	0.11	0.05	0.661*	5.59	5.49	0.435*	6.83	7.16	0.663*
Pine species	0.12	0.06	0.694*	6.79	6.64	0.575*	8.36	8.74	0.300*
SB	51.00	52.27	0.156*	17.59	17.02	0.158†	4.58	3.39	0.556*
SW	1.26	1.26	0.100*	1.22	1.08	0.450*	1.66	1.66	0.757*
Spruce species	52.26	53.52	0.183*	18.81	18.09	0.046†	6.24	5.06	0.917*
Other	0.05	0.03		0.04	0.05		0.15	0.12	

Note: See Table 1 for species and species group abbreviations; np, not present.

*Wilcoxon's signed ranks test.

†Paired t test on transformed data.

OLS data. Larch seems to have almost completely disappeared from SR4E and SR5E and has also decreased significantly in SR3E (Table 4). Other conifers, such as hemlock, spruce species, and balsam fir also were significantly reduced in abundance. Interestingly, the latter had a significant change in SR5E, but the overall abundance of the species remained the same, suggesting a change at the stand level. Effect sizes for the dominant species analysis ranged from 0.4% to 2.9% for the three SRs; from 1.8% to 2.9% for species compositions >10%; and from 0.4% to 1.7% for compositions between 1% and 10%. We had no power to detect differences for compositions <1% (effect sizes could not be calculated).

Most species also changed significantly based on the ranked and equal abundance importance values (Table 5). Based on the ranked abundance importance values, only balsam fir and oak species in SR3E; cedar, hemlock, jack pine, and spruce species in SR4E; and beech in SR5E did not change significantly. Based on the equal abundance importance values, only oak species in SR3E; cedar, hemlock, and jack pine in SR4E; and balsam fir and beech in SR5E did not change significantly.

If the equal abundance (proportion of species or species groups within each boundary expressed as a percentage of the total length in each data set) is not significantly different between the OLS and FRI data, then the change is more a factor of dominance than of frequency. Conversely, if the ranked abundance is not significantly different, then the change is more a factor of frequency than dominance. All hardwoods individually (except ash) and hardwoods overall showed an upward trend in dominance. On the other hand, conifers showed an overall significant downward trend (Table 6).

A reasonable logistic regression model (93.7% classification accuracy, $\chi^2 = 1683.2$, $p < 0.01$) was obtained and used to separate unspecified birch in the OLS into white and yellow birch. Only about 25% of 5091 birch stands were identified to species by the land surveyors; the other 75% were ambiguous or only identified to genus (i.e., birch species or boileau). Analyses by dominant species and ranked and equal abundance importance values all show an increase in white birch and a decrease in yellow birch (Table 7).

When species were grouped into functional categories, a significant ($p < 0.001$) decrease in conifers and increase in intolerant hardwoods was evident for all three SRs (Fig. 2). Midtolerant to tolerant hardwoods in SR4E and SR5E also increased significantly.

There is evidence in the OLS data to indicate that a small amount of logging was encountered during these surveys in the three SRs. A total of 43.2 km (0.21% of the study area)

Table 4. Comparison of dominant species composition in OLS and FRI.

	SR3E			SR4E			SR5E		
Species or species group	OLS (1887–1955)	FRI (1998–2006)	*p* ($\alpha = 0.05$)	OLS (1857–1945)	FRI (1998–2004)	*p* ($\alpha = 0.05$)	OLS (1816–1934)	FRI (1998–2009)	*p* ($\alpha = 0.05$)
A	0.02	na		0.04	na		0.37	na	
AB	0.06	0.01		0.40	0.02		0.59	0.61	
AW	np	np		np	np		0.01	0.04	
Ash species	0.08	0.01	0.000*	0.44	0.02	0.000*	0.97	0.65	0.000*
AL	2.04	na		0.95	na		1.99	na	
BE	0.01	np	0.180*	np	np		2.52	0.19	0.000*
BF	3.48	2.71	0.003*	4.08	2.29	0.000*	5.26	5.25	0.014*
BIR	4.46	na		9.41	na		8.27	na	
BL	np	na		0.15	na		0.07	na	
BW	1.91	10.33		3.25	26.93		1.49	8.51	
BY	0.02	0.07		0.11	1.29		1.04	3.08	
Birch species	6.39	10.40	0.000*	12.92	28.22	0.000*	10.87	11.59	0.221*
CE	1.99	2.22†	0.154*	2.59	2.45†	0.103*	6.14	3.48	0.000*
HE	np	np		0.05	0.02	0.686*	7.76	2.46	0.000*
LA	2.80	1.21	0.000*	2.38	0.10	0.000*	3.82	0.24†	0.000*
M	0.03			2.04	na		16.79	na	
MH	<0.01	0.05		0.04	5.00†		0.37	34.68	
MS	0.01	0.05		0.02	0.93†		0.02	4.57	
Maple species	0.04	0.10	0.023*	2.10	5.92	0.000*	17.18	39.25	0.000*
O	np	na		np	na		0.11	na	
OB	np	np		np	np		0.06	np	
OR	np	np		np	0.17		0.03	3.65	
OW	np	np		np	np		np	0.05	
Oak species	np	np		np	0.17	0.000*	0.21	3.70*	0.000*
PJ	15.22	11.32	0.000*	21.16	20.85	0.445*	1.20	2.01	0.000*
PO	9.64	19.92	0.000*	7.24	14.08	0.000*	7.91	16.71	0.000*
P	0.16	na		4.85	na		14.31	na	
PR	0.14	0.02		3.41	1.22		1.97	1.65	
PW	0.36	0.10		9.30	5.95		2.06	7.08	
Pine species	0.67	0.11	0.000*	17.57	7.17	0.000*	18.34	8.73	0.000*
SP	56.35	na		26.93	na		5.29	na	
SB	0.42	50.62		0.71	17.45		0.60	3.88	
SR	0.27	np		0.02	np		0.03	np	
SW	0.06	1.33		np	1.24		<0.01	np	
Spruce species	57.10	51.95	0.000*	27.65	18.69†	0.000*	5.92	5.53	0.945*
H	<0.01	np		0.62	np		8.12	0.01	
MT	0.01	na		0.09	na		1.28	na	
Other‡	0.79	0.04		0.18	0.03		0.54	0.21	

Note: Because not all ash, birch, maple, oak, pine, and spruce were recorded by species in the OLS, all entries were also grouped at the genus level. Wilcoxon's signed ranks test was used to test for statistical significance beween the FRI and OLS data. na, not applicable, no analysis was performed; np, not present.

*Wilcoxon's signed ranks test.

†We were not able to state with certainty that the changes found along township boundaries for these species reflect changes to the whole forest area (Table 3).

‡The "other" group includes dominant species with <1% of forest composition (Table 2).

was identified in the OLS data as cutover. Agricultural and settlement clearings at the time of the OLS accounted for only 0.08% (17.1 km) of the forest.

Discussion

Studies that use land survey notes to describe the preindustrial forest assume that a sample of the township grid or lots and concessions is sufficient to describe the composition of the whole forest (e.g., Jackson et al. 2000; Leadbitter et al. 2002; Suffling et al. 2003). This is not always the case. Species distribution and abundance play a role in how valid sampling along a township grid is in describing tree species composition for a whole forest. Spruce species in SR4E, although quite abundant in the present-day forest, is sufficiently variable that simply sampling along a township grid is insufficient to describe the overall abundance in that SR. Other species that have statistically different compositions between the sample along the township grid and the whole SR were species that were not common (i.e., cedar and larch).

The period up to the time the OLS were conducted in our study area is evidenced by limited logging (0.21% of the study area) and land clearing (0.08% of the study area). These results indicate that the OLS describes a forest composition that would have been influenced primarily by preindustrial processes and events. After the OLS were recorded, logging and land clearing for agriculture and other human

Table 5. Comparison by importance value (i.e., ranked or equal abundance) between OLS and FRI data.

Species or species group	SR3E ranked OLS	SR3E ranked FRI	SR3E ranked *p*	SR3E equal OLS	SR3E equal FRI	SR3E equal *p*	SR4E ranked OLS	SR4E ranked FRI	SR4E ranked *p*	SR4E equal OLS	SR4E equal FRI	SR4E equal *p*	SR5E ranked OLS	SR5E ranked FRI	SR5E ranked *p*	SR5E equal OLS	SR5E equal FRI	SR5E equal *p*
A	0.02	na		0.02	na		0.07	na		0.08	na		0.51	na		0.55	na	
AB	0.10	0.03		0.12	0.03		0.45	0.05		0.48	0.07		0.59	0.98		0.60	1.05	
AW	<0.01	np		<0.01	np		0.01	np		0.01	np		0.02	0.42		0.02	0.56	
Ash species	0.11	0.03	0.000*	0.14	0.03	0.000*	0.53	0.05	0.000*	0.57	0.07	0.000*	1.11	1.39	0.000*	1.17	1.61	0.001*
AL	3.60	na		4.47	na		1.06	na		1.13	na		2.20	na		2.35	na	
BE	0.01	np	0.068*	0.01	np	0.068*	np	<0.01	0.180*	np	<0.01	0.180*	3.02	2.66	0.518*	2.98	3.03	0.651*
BF	7.98	7.75	0.019*	9.56	9.05	0.154*	9.68	6.39	0.000*	11.22	7.84	0.000*	8.00	8.10	0.321*	9.21	8.61	0.083*
BIR	6.83	na		7.63	na		12.72	na		13.55	na		11.13	na		11.31	na	
BL	<0.01	na		<0.01	na		0.17	na		0.17	na		0.25	na		0.27	na	
BW	3.03	10.68		3.45	10.67		3.53	20.61		3.71	18.18		2.18	9.52		2.17	9.44	
BY	0.02	0.07		0.03	0.07		0.16	1.95		0.16	2.10		1.19	7.29		1.12	7.94	
Birch species	9.88	10.75	0.102*	11.11	10.74	0.002*	16.58	22.56	0.000*	17.60	20.28	0.000*	14.75	16.81	0.000*	14.87	17.38	0.000*
CE	2.92	3.84[†]	0.000*	3.35	4.47[†]	0.000*	3.36	3.17[†]	0.130*	3.82	3.37[†]	0.385*	6.58	3.28	0.000*	6.87	3.34	0.000*
HE	<0.01	np	0.317*	<0.01	np	0.317*	0.06	0.04	0.865*	0.07	0.05	0.396*	7.74	3.61	0.000*	7.63	4.27	0.000*
LA	7.47	4.38	0.000*	8.50	5.41	0.000*	3.07	0.62	0.000*	3.33	0.81	0.000*	4.19	0.54[†]	0.000*	4.30	0.64[†]	0.000*
M	0.11	na		0.15	na		1.77	na		1.76	na		12.13	na		10.47	na	
MH	0.01	0.05		0.01	0.05		0.07	2.97		0.10	2.41		0.25	18.39		0.22	13.38	
MS	0.01	0.23		0.02	0.31		0.04	3.43		0.05	4.51		0.03	8.52		0.05	9.99	
Maple species	0.13	0.28	0.000*	0.18	0.36	0.000*	1.88	6.40	0.000*	1.90	6.93	0.000*	12.42	26.91	0.000*	10.74	23.37	0.000*
O	np	na		np	na		0.01	na		0.02	na		0.19	na		0.23	na	
OB	np	np		np	np		np	np		np	np		0.05	np		0.06	np	
OR	<0.01	<0.01		<0.01	<0.01		<0.01	0.25		0.01	0.28		0.06	3.77		0.07	3.78	
OW	np	np		np	np		np	np		np	np		<0.01	0.09		<0.01	0.11	
Oak species	<0.01	<0.01	0.655*	<0.01	<0.01	0.655*	0.02	0.25	0.000*	0.02	0.28	0.000*	0.31	3.86	0.000*	0.37	3.88	0.000*
PJ	11.62	10.02	0.000*	10.58	9.55	0.000*	15.46	15.64	0.566*	13.85	13.99	0.605*	1.12	1.75	0.000*	1.13	1.65	0.000*
PO	11.32	17.09	0.000*	11.62	16.20	0.000*	8.65	13.55	0.000*	9.12	13.23	0.000*	5.58	12.52	0.000*	4.86	11.15	0.000*
P	0.18	na		0.19	na		4.03	na		4.03	na		12.10	na		11.91	na	
PR	0.13	0.03		0.14	0.04		3.18	1.48		2.93	1.55		1.54	1.87		1.39	2.04	
PW	0.40	0.15		0.47	0.19		7.47	6.48		7.19	6.89		2.03	6.76		2.01	6.96	
Pine species	0.71	0.18	0.000*	0.79	0.22	0.000*	14.69	7.95	0.000*	14.15	8.44	0.000*	15.67	8.62	0.000*	15.30	9.00	0.000*
SP	42.48	na		37.73	na		23.19	na		21.29	na		5.62	na		5.66	na	
SB	0.46	41.84		0.44	38.97		0.61	17.92		0.58	17.50		0.79	3.42		0.81	3.35	
SR	0.23	np		0.22	np		0.02	np		0.03	np		0.05	<0.01		0.02	<0.01	
SW	0.04	3.78		0.03	4.91		<0.01	5.40		<0.01	7.17		0.01	4.71		0.02	6.39	
Spruce species	43.22	45.62	0.000*	38.42	43.88	0.000*	23.83	23.32[†]	0.831*	21.90	24.67[†]	0.000*	6.46	8.13	0.000*	6.51	9.74	0.000*
H	0.02	np		0.02	np		0.65	np		0.69	np		7.32	np		7.18	0.02	
MT	0.02	na		0.01	na		0.09	na		0.09	na		1.22	na		1.21	na	
Other	1.21	0.07		1.45	0.08		0.43	0.06		0.58	0.06		1.91	0.91		2.65	1.23	

Note: Since not all ash, birch, maple, oak, pine and spruce were recorded by species in the OLS, all entries were also grouped at the genus level. See Table 1 for and species group abbreviations. na, not applicable, no analysis was performed; np, not present. II Wilcoxon's signed ranks test; paired *t* test on transformed data; np, not present

*Wilcoxon's signed ranks test.

[†]We were not able to state with certainty that the changes found along township boundaries for these species reflect changes to the whole forest area (Table 3).

Table 6. Increase or decrease in dominance and (or) frequency of occurrence of tree species in the forest today based on ranked and equal abundance importance values from Table 5.

	SR3E			SR4E			SR5E		
Species or species group	Ranked	Equal	Interpretation	Ranked	Equal	Interpretation	Ranked	Equal	Interpretation
Hardwoods									
Ash species	↓*	↓*	Less dominance and frequency	↓*	↓*	Less dominance and frequency	↑*	↑*	More dominance and frequency
Birch species	↑*	↓*	More dominance and less frequency	↑*	↑*	More dominance and frequency	↑*	↑*	More dominance and frequency
Maple species	↑*	↑*	More dominance and frequency	↑*	↑*	More dominance and frequency	↑*	↑*	More dominance and frequency
Oak species	np	np	—	↑	↑	—	↑*	↑*	More dominance and frequency
Poplar	↑*	↑*	More dominance and frequency	↑*	↑*	More dominance and frequency	↑*	↑*	More dominance and frequency
All hardwood‡	↑*	↑*	More dominance and frequency	↑*	↑*	More dominance and frequency	↑*	↑*	More dominance and frequency
p	0.000	0.000		0.000	0.000		0.000	0.000	
Conifers									
Balsam fir	↓	↓*	Less frequency	↓*	↓*	Less dominance and frequency	↑	↓	—
Cedar	↑†	↑†	More dominance and frequency	↓†	↓†	—	↓*	↓*	Less dominance and frequency
Larch	↓*	↓*	Less dominance and frequency	↓*	↓*	Less dominance and frequency	↓†	↓†	Less dominance and frequency
Jack pine	↓*	↓*	Less dominance and frequency	↑	↑	—	↑*	↑*	More dominance and frequency
Pine species	↓*	↓*	Less dominance and frequency	↓*	↓*	Less dominance and frequency	↓*	↓*	Less dominance and frequency
Spruce species	↑*	↑*	More dominance and frequency	↓†	↑†	More frequency	↑*	↑*	More dominance and frequency
All conifer §	↓*	↑	Less dominance	↓*	↓*	Less dominance and frequency	↓*	↓*	Less dominance and frequency
p	0.000	0.331		0.000‖	0.000		0.000	0.000	

Note: np, not present.

*Significant Wilcoxon's signed ranks test from Table 5.

†We were not able to state with certainty that the changes found along township boundaries for these species reflect changes to the whole forest area (Table 3).

‡Hardwood species included ash species, BE, birch species, maple species, oak species, and PO.

§Conifer species included BF, CE, HE, LA, PJ, pine species, and spruce species (CE was excluded in SR3E, CE and spruce species were excluded in SR4E, and LA was excluded in SR5E; Table 3).

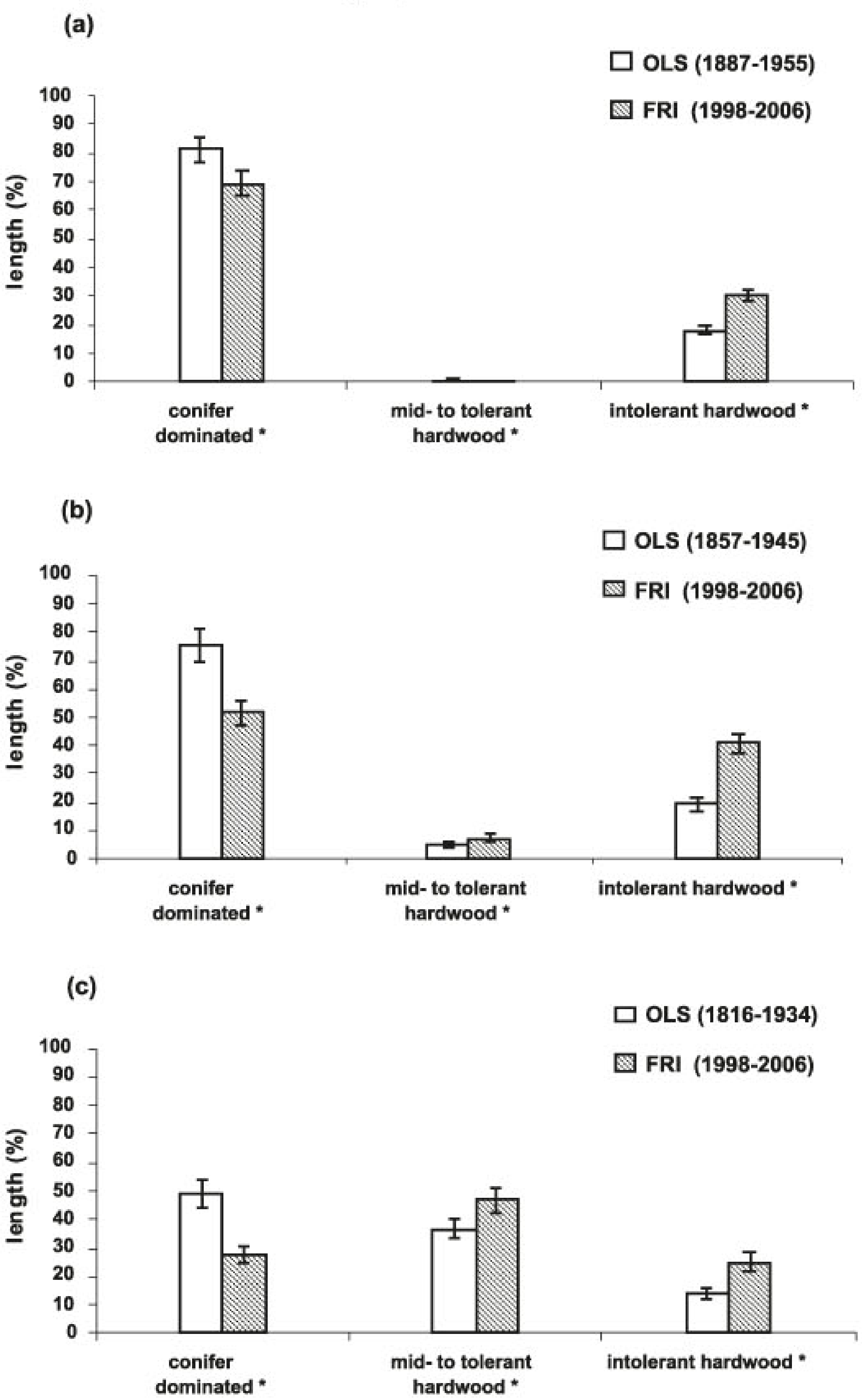
‖A t test was performed on transformed data; Wilcoxon signed ranks tests were used to determine all ofther p values.

Table 7. OLS data showing changes in dominant species composition and importance values, i.e., ranked or equal abundance, after using logistic regression models to predict the presence of white (BW) and yellow birch (BY) where the OLS data only described these trees as birch or boileau.

	Dominant species			Ranked			Equal		
Site region and species	OLS	FRI	p*	OLS	FRI	p	OLS	FRI	p
SR3E									
BW	5.90	10.33	0.000*	9.35	10.68	0.000*	10.58	10.67	0.423*
BY	0.49	0.07	0.000*	0.53	0.07	0.000*	0.53	0.07	0.000*
SR4E									
BW	10.94	26.71	0.000*	14.24	20.61	0.000*	15.32	18.18	0.000*
BY	1.97	1.29	0.011*	2.33	1.95	0.087*	2.27	2.10	0.541*
SR5E									
BW	3.71	8.51	0.000*	5.35	9.52	0.000*	5.40	9.44	0.000*
BY	7.17	3.08	0.000*	9.39	7.29	0.000*	9.45	7.94	0.000*

*The p values were determined using Wilcoxon's signed ranks test.

Fig. 2. Broad tree categories based on dominant species and logistic regression codes for birch for (*a*) SR3E, (*b*) SR4E, and (*c*) SR5E. Wilcoxon's signed ranks test was used to compare related proportions ($p < 0.001$ for all samples).



needs became much more prevalent; the majority of our study area is available for logging. Therefore, the current forest composition of our study area is influenced by industrial activity. Other studies in similar forest regions in Ontario (Jackson et al. 2000; Leadbitter et al. 2002; Suffling et al. 2003) and in the US Lakes States (Whitney 1987; Cole et al. 1998, Radeloff et al. 1999) show no change or a statistically significant increase in poplar, maple, and oak as a dominant species in the forest today. These results match those that we find in our study. Results from other research that use historic land surveyor data are consistent with ours and show no change or a reduction in stands dominated by tamarack (Suffling et al. 2003), hemlock (White and Mladenoff 1994; Abrams and Ruffner 1995), and red and white pine (Whitney 1987; Radeloff et al. 1999).

Our results show an increase in white birch and a decrease in yellow birch contrary to the results of Leadbitter et al. (2002), whose study areas lies within ours. The difference may be due to the specific areas sampled or due to the differences in approach (a logistic regression model versus classification by expert opinion) used to classify transects that were simply recorded as "birch."

The changes in abundance based on both the dominant species and importance values between the OLS and FRI data sets for the three SRs suggest the occurrence of events that limited the regeneration and growth of conifers and favoured the regeneration and growth of white birch, poplars, oak, and maples. Possible explanations for these changes are preferential harvesting of conifers and the lack of regeneration and maintenance effort, forest fire suppression, and exotic insect and disease infestations particularly white pine blister rust (Maloy 1997; Campbell and Antos 2000) and European larch sawfly (*Pristiphora erichsonii* Hartig; Girardin et al. 2001).

Forestry operations prior to the implementation of the Crown Forest Sustainability Act (Province of Ontario 1994) on public lands in Ontario emphasized the removal of economically valuable stems (in most cases, the best seed producers) of conifers and some hardwoods. This approach was common in the past. The removal of large seed-bearing trees by logging would decrease the regeneration potential of these tree species (Russell et al. 1993) while favouring the regeneration of hardwood tree species capable of vegetative reproduction (e.g., poplar). The logging, particularly if intensive, may have destroyed established regeneration, whereas the impact of past horse logging may have been more benign. Fires after early logging may also have destroyed established regeneration.

Fire regime affects tree species distribution. For example, Flannigan and Bergeron (1998) show that red pine is restricted to fire-sheltered locations in the boreal forest. In the past, logging slash often supported fires that destroyed potential regeneration and further damaged or killed seed trees (Whitney 1987; Radeloff et al. 1999). Radeloff et al. (1999) also noted that salvage logging during budworm (*Choristoneura* spp.) outbreaks may aggravate this increase in fire potential. Whitney (1987) noted that, in northern Michigan, harvesting of desired species (white pine initially, then eastern hemlock and better quality hardwoods) and fire suppression allowed tree species capable of regenerating vegetatively or through the production of large amounts of seed, such as oak, trembling aspen, white birch, and jack pine, to flourish and create a new forest. Further, Jackson et al. (2000) stated that the change in the boreal forest from conifer-dominated stands to stands of intolerant hardwoods may be attributed to clearcut harvesting with little follow up regeneration treatments. Cole et al. (1998) attributed the decline in the pine forests (ca. 21%) of the Great Lake States to logging.

White birch and poplars are both well adapted to frequently producing large numbers of wind-dispersed seed as well as sprouting and suckering vigorously, respectively, after harvesting or a fire (Burns and Honkala 1990). An increase in white birch in the forest today is further supported by the logistic regression model results (Table 7). Past harvesting in maple stands targeted well-formed stems with little rot, and left poor-quality maple standing and able to regenerate areas to maple. Fire-suppression efforts over the past 80 years would also have favoured maples over associated species, such as yellow birch and eastern hemlock (Dahir and Lorimer 1996; Leadbitter et al. 2002). Fires would burn off the undecomposed fallen maple leaves that form a physical and chemical barrier to the regeneration of other tree species but not to maple seeds, whose vigorous radicle penetrates easily to the soil and enables this genus to regenerate sites beneath their parent trees despite a thick layer of undisturbed litter (Burns and Honkala 1990; Frelich 1995). Leadbitter et al. (2002) also noted a significant increase in the abundance of maple with an increase of almost 17% in Algonquin Park from 1890 to 1990. This increase in maples and intolerant hardwoods is consistent with the findings of other studies based on surveyor records (Radeloff et al. 1999; Jackson et al. 2000) and in more recent field surveys (Hearndon et al. 1992; Carleton and MacLennan 1994). Although the increased abundance of intolerant hardwoods and oak could have occurred largely in response to fire, the increase in maples contradicts this idea because maples benefit from fire suppression. This suggests that logging and fire suppression may have played a more dominant role than fire in initiating these changes in Ontario.

Severe infestations by the eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) in the 1980s or earlier is likely to have reduced the area and importance value of balsam fir within stands. These reductions were indeed found in SR3E and SR4E, suggesting that budworm defoliation may have played a role in the reduced dominance of balsam fir in addition to spruce. Similarly, an outbreak of the European larch sawfly, an introduced insect defoliator, may have played a dominant role in decimating larch populations in northeastern Ontario in the late 1800s and early 1900s, particularly in upland sites (Howse 1983). In Minnesota, 1×10^9 board feet (1000 board feet = 2.360 m^3) were lost as a result of this defoliator from 1910 to 1926 (Baker 1972). The first record of an outbreak in Canada was in the Quebec City area in the early 1880s (Girardin et al. 2005). The decrease in abundance and frequency of larch stands in all SRs could be attributed to these defoliation events. Unlike in coniferous stands, outbreaks of defoliating insects, such as the forest tent caterpillar (*Malacosoma disstria* Hbn.), in deciduous forests do not seem to have reduced the abundance of white birch, poplars, or maples.

Logging may also have been a factor in the reduction of larch abundance and frequency. In the early 1880s, the Canadian Pacific Railway (CPR) opened up into northern Ontario and with it arose the need for railway ties, in which primarily larch and cedar were used. Larch was preferred for railway ties because it holds nuts and bolts better than any other resinous species (Lutz 1997). In the 19th century, larch was also used extensively for shipbuilding purposes. Along with tanbark (hemlock), cedar posts, and telegraph poles, large volumes larch railway ties were harvested in throughout northern Ontario from 1893 to 1903 (Cameron 1902; Gunning 1998). Railways, such as the Temiskaming and Northern Ontario railway, are constructed to follow the height of land and, as such, would be cutting ties from upland forests, which contributed to reductions in larch; however, this would be minor compared with the impact of widespread insect defoliation.

There is some evidence in the OLS notes to indicate that small amounts of logging had occurred on several township boundaries. In areas along the CPR and in Algonquin Park, the first wave of logging had already passed through in Ontario. J.R. Booth purchased the timber berth that became Algonquin Park in 1858 and logged it for 77 years (Gillis and Roach 1984) during the same time (1858–1895) when most of this area was surveyed. In 1870, J.R. Booth's company had an output of 30×10^6 board feet of pine in the Nipissing District (Gunning 1998). Overall, the extent of harvesting and agricultural development observed in the surveys was minimal; suggesting that wide-scale land clearing and logging had not yet taken place by the time of the surveys.

Conclusions

The comparison of forest compositions in the OLS records and those in the current FRI showed changes in species composition that differed from what might have resulted if natural disturbance was still the primary cause of change in central and northeastern Ontario. Forest managers can use the preindustrial tree species abundances described in this report to help develop species-diversity objectives and strategies for species restoration or reduction in their forest management plans but must do so with caution. Some factors, such as climate and the effects of native and introduced insects and diseases, have changed over time. To use the template for preindustrial forest composition, managers must first understand the context under which the preindustrial forest established itself and the context under which their current forest will become established and grow.

Stand data from the OLS records provide an invaluable source of information to help develop a template for the composition of the preindustrial forest. The OLS records for the site regions provided a statistically adequate sample to describe the preindustrial abundance of all tree species except for cedar in SR3E, cedar and spruce species in SR4E, and larch in SR5E.

Historical data from 1816 to 1955 for the site regions suggest that today's forest composition is significantly different from that in the past. Economically valuable species, such as white pine, red pine, and the spruces, as well as tree species with a shorter history of industrial use, such as cedar and larch, have decreased in abundance. The changes in cedar and balsam fir may be more a factor of differences between the OLS and the current FRI. The reduced abundance of larch was probably caused by the introduction of the European larch sawfly, an insect defoliator, in the 1880s. We suggest that the changes in the abundance of economically valuable tree species have resulted from logging, fire suppression, and (or) inadequate regeneration effort. The reduction in the abundance of these valuable timber species and the concomitant increase in the abundance of intolerant hardwoods, oaks, and maples are changes that might not have occurred if only natural disturbance had been responsible for the current landscape.

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