Spatial distribution of forest landscape change in western New York from presettlement to the present

Yi-Chen Wang, Barry J. Kronenfeld, and Chris P.S. Larsen

Abstract: Changes in tree taxon composition and distribution in western New York over a 200 year time period ca. 1797–1993 were examined by comparing the presettlement land survey with the US Forest Inventory and Analysis (FIA) survey. To ensure data quality, biases in presettlement bearing tree selection and FIA plot location were assessed. A 6 mile × 6 mile grid of taxa abundance was then estimated using geostatistics. Overall, significant changes in taxon composition occurred, with the taxa most abundant in the presettlement land survey — beech (37.0%), sugar maple (21.0%), and eastern hemlock (8.3%) — being replaced by sugar maple (19.2%), ash (11.7%), and red maple (11.4%) in the FIA survey. Spatially resolved comparisons showed that the landscape changed from fairly spatially homogeneous to more heterogeneous; in the presettlement survey, the most abundant taxon in most of the 6 mile × 6 mile grid cells was beech, while in the present survey, the most abundant taxon in most of the cells was one of several early successional taxa that each displayed a distinctly clustered geographic pattern of dominance. The clusters of dominance of the different early successional taxa may correspond to environmental factors. This study demonstrates the insights available through spatially resolved analyses of changes in the forest landscape between presettlement and present.

Résumé : Les changements dans la distribution et la composition des taxons de la végétation arborescente survenus au cours de la période d'environ 200 ans, de 1797 à 1993, dans l'ouest de l'État de New York ont été étudiés en comparant les relevés d'arpentage effectués avant la colonisation et ceux du Programme national d'inventaire et d'analyse des forêts des États-Unis (FIA). Afin d'obtenir des données fiables, les biais de la sélection des arbres de direction avant la colonisation et de la localisation des placettes échantillons des relevés du Programme FIA ont été évalués. L'abondance des taxons de chacune des cellules (6 milles × 6 milles) d'une grille a ensuite été évaluée à l'aide de la géostatique. Dans l'ensemble, des changements importants sont survenus dans la composition des taxons: les taxons les plus abondants avant la colonisation, soit le hêtre (37,0 %), l'érable à sucre (21,0 %) et la pruche du Canada (8,3 %), ont été actuellement remplacés par l'érable à sucre (19,2 %), le frêne (11,7 %) et l'érable rouge (11,4 %) dans les relevés du Programme FIA. Des comparaisons spatiales ont montré que le paysage autrefois d'apparence plus homogène sur le plan spatial est devenu plus hétérogène. Avant la colonisation, le hêtre était le taxon le plus abondant dans la plupart des cellules de 6 milles × 6 milles. Aujourd'hui, le taxon le plus abondant du relevé de la plupart des cellules est l'un ou l'autre de la multitude des taxons du début de succession et la distribution géographique de la dominance de chacun de ces taxons prend clairement la forme de grappes. Les grappes de dominance des différents taxons du début de succession seraient le reflet de l'effet des facteurs environnementaux. Cette étude donne un aperçu des possibilités qu'offre l'analyse spatiale en montrant les changements survenus dans le paysage forestier depuis les débuts de la colonisation.

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Introduction

Description and quantification of ecological patterns, both spatial and temporal, are key steps to understanding ecological processes and to disentangling the complexity of natural systems (Fortin and Dale 2005). Reconstructing the spatial extents of natural phenomena at different time periods to document how much landscape change has been induced by humans is a fundamental goal of ecologists (Certain et al. 2007). In many parts of the world, human settlement and its expanding demands have substantially modified the landscape. Large-scale changes to forest composition and structure directly influence floral and faunal habitats. For sustainable ecosystem management, investigation of forest change is needed to provide insights into the development processes that have given rise to the current forests.

To investigate forest change, knowledge of historical forest conditions that can act as baselines is desirable, particularly in regions lacking remnants of primary or old-growth forests. In North America, forest conditions before major

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Y.-C. Wang.[1] Department of Geography, National University of Singapore, 117570 Singapore.
B.J. Kronenfeld. Department of Geography and Geoinformation Science, George Mason University, Fairfax, VA 22030, USA.
C.P.S. Larsen. Department of Geography, University at Buffalo, The State University of New York, Buffalo, NY 14261, USA.

[1] Corresponding author (e-mail: geowyc@nus.edu.sg).

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European settlement have often been used as a basis for ecological studies (Wang 2005). An invaluable source of information has been the presettlement land survey records (PLSRs) that were collected between the late 17th and the early 20th centuries for land sale and settlement (Whitney 1996). Although the data were not originally collected for ecological purposes, they provide a representation of the landscape that existed prior to significant European settlement. Wang (2005) has thoroughly discussed the characteristics and data quality issues of the PLSRs and various types of ecological analysis based on the data.

Tree species occurrences in the PLSRs have often been compared with those in current forest surveys to examine forest change. Current forest surveys are either conducted by researchers through fieldwork (e.g., Nelson et al. 1994; Cowell and Jackson 2002) or obtained from recent forest census databases, such as the Forest Inventory and Analysis (FIA) Program of the US Department of Agriculture (USDA) Forest Service (e.g., Radeloff et al. 1999; Dyer 2001; Leahy and Pregitzer 2003; Friedman and Reich 2005) and the Ontario Forest Resource Inventory of Canada (e.g., Jackson et al. 2000). The FIA data are most commonly used by PLSR researchers because of their wide coverage throughout the country, allowing changes to be investigated at the landscape scale.

The comparison of forest structure and pattern derived from PLSRs and the FIA data, however, is not straightforward because the two surveys have different sampling schemes. Most of the PLSRs record two to four bearing trees at survey corners at regular intervals ranging from 0.5 to 6 miles (1 mile = 1.609 km) along the survey lines. In contrast, the FIA inventory consists of plots of approximately 1/6 acre (1 acre = 0.405 ha), within which all trees are inventoried. Although the exact plot area and spacing varies by state and sampling period, density is generally at least one plot per 92.16 km^2 (Hansen et al. 1992). Therefore, the PLSRs are a relatively dense network of sample locations, but fewer trees are sampled per location; the FIA data are a relatively sparse network of sample locations, but more trees are sampled per location. The comparability of the PLSR and the FIA data thus needs to be evaluated, and methods that can incorporate the two different sampling schemes are desirable to achieve a more accurate comparison of the landscapes from which they came (Wang 2005).

The goal of this paper is to investigate changes of forest species composition and spatial pattern between the times of the PLSR and the FIA surveys in western New York. This particular study area was surveyed by a private land company, which followed many but not all of the practices of the later General Land Office (GLO) surveys (Wyckoff 1988). In this sense, the private land survey records of western New York broadly represent both the public GLO surveys from Ohio to California in which a regular survey system was employed and a subset of the early surveys of the northeastern USA (e.g., Maine) in which the survey pattern was rectilinear but tree diameters were not recorded (Wang 2005).

The study area sits in the middle of a zone extending approximately from Wisconsin to Maine of which several studies have noted a decrease in the formerly prominent American beech (*Fagus grandifolia* Ehrh.) to less than 14% of its presettlement median values following European settlement (i.e., Whitney 1996, pp. 159 and 196; Bürgi et al. 2000; Whitney and DeCant 2003). In contrast, studies in adjacent areas of southeastern Ohio (Dyer 2001) and southern New England (Bürgi et al. 2000) have shown a former dominance of white oak (*Quercus alba* L.), which has decreased to less than 27% of its presettlement median values. It would be desirable to know if western New York has experienced changes similar to either or both of these regions. A previously published study of western New York only analyzed small portions of the study area and compared aggregate, nonspatial data of forest compositional change in tabular form (Gordon 1940). A broad-scale spatially resolved comparison of the presettlement and current forest landscapes, just as those done in the Midwest using the PLSR and FIA data (e.g., Radeloff et al. 1999; Friedman and Reich 2005), is needed that visualizes covariation between vegetation and environment and identifies where vegetation composition has changed the most.

Because spatial analysis requires stringent examination of data quality, we first examined the comparability of the PLSR and the FIA surveys so that a more accurate comparison of the forest conditions derived from the two data sets could be made. We then compared species composition between ca. 1797 and 1993 and characterized the spatial patterns of the forest landscape in both time periods and identified the kind of change that occurred.

Study area and data

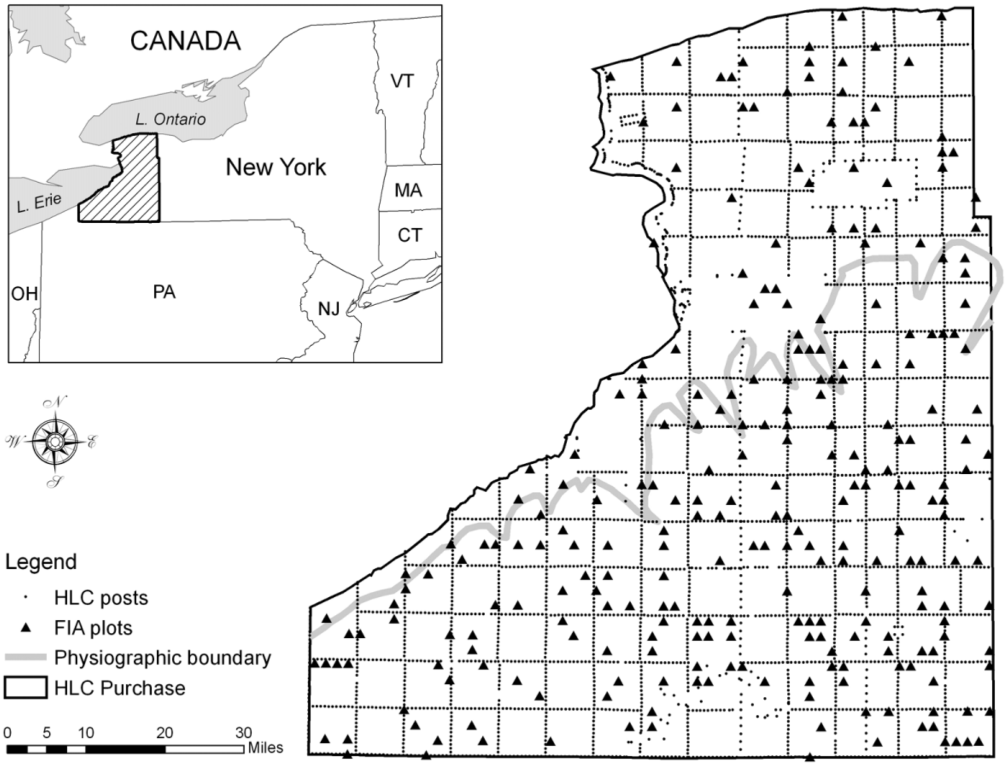
Study area

The study area is the Holland Land Company (HLC) Purchase of western New York (Fig. 1). It lies between the Pennsylvania state line to the south and Lake Ontario to the north, and is bordered on the west by Lake Erie and the Niagara River. The area covers approximately 14 400 km^2, extending across two commonly recognized physiographic sections. The Erie–Ontario Lowland in the northern part of the study area is a section with relatively low, flat topography; the Appalachian Upland in the south has a topography of dissected uplands, mostly glaciated (Fenneman 1938). The presettlement vegetation was dominated by beech and sugar maple (*Acer saccharum* Marsh.) (Wang 2007).

Presettlement land survey records

The presettlement land surveys of western New York were conducted by the HLC, a private company. The HLC acquired, divided, and surveyed the land of this area in preparation for settlement. Land was divided into townships of 4 miles × 6 miles, 6 miles × 6 miles, and 7 miles × 6 miles, and was in turn subdivided into lots ranging from 40 to 640 acres. Posts were erected at 0.5 mile intervals along the township survey lines. Neighboring trees, known as bearing trees, were blazed and inscribed to mark the locations of the survey posts. Surveyors recorded the species of bearing tree, as well as the distance and direction between each tree and its designated post. Estimated tree diameters were recorded in the GLO surveys but, similar to many other private land surveys and to the earlier metes and bounds surveys, were not found in the HLC survey used in this study. The locations and species of 8792 tallied bearing trees and their des-

Fig. 1. Location of study area in western New York, USA. The grey line indicates the physiographic boundary between the Erie–Ontario Lowland in the north and the Appalachian Upland in the south. HLC, Holland Land Company; FIA, Forest Inventory and Analysis. 1 mile = 1.609 km.



ignated posts along the township perimeter surveys between 1797 and 1799 were transcribed from the handwritten “Range Books,” available on microfilms at the HLC Archives at SUNY Fredonia and the New York State Archives at Albany, New York. Data quality issues of the HLC township surveys for vegetation reconstruction have been examined in Wang (2005, 2007).

Current forest surveys

The current forest conditions are derived from FIA surveys, an ongoing inventory of forest timber resources in the United States (USFS (United States Department of Agriculture, Forest Service) 2007). Data were taken from the most recent complete inventory of New York State, conducted between 1991 and 1993. Information on individual trees included species, diameter at breast height (dbh), and expansion factors that express the number of trees per hectare (TPH) represented by a given tree in the database, determined by the effective sampling area. The database also includes estimates of forest stands made by inventory workers in the field. Although these estimates are necessarily imprecise, they provide a general means of differentiating between young pioneer and mature forest stands.

Of a total of 764 FIA plot records within the study area, we removed 18 that were marked as being of artificial origin, 425 that contained no trees, and another 27 that contained no trees with a dbh ≥9 in. (discussed below); data from an additional 33 plots were aggregated with other plots with which they were co-located. This resulted in a total of 261 plots containing 4303 trees with a dbh ≥9 in. (Fig. 1). The density of FIA plots differed significantly between the Appalachian Upland (one per 49 km^2) and the Erie–Ontario Lowland (one per 81 km^2). The size of the individual FIA survey plots and the sampling methods used have varied somewhat historically and by state, but from expansion factors contained in the data, it can be inferred that western New York was inventoried using a combination of 0.5 ha fixed-area plots and variable-area sampling using a 15 basal area factor prism. Although differences in sample density and sampling scheme may affect levels of uncertainty, they would not introduce any systematic bias into our analysis.

One idiosyncrasy of the FIA data that affects any type of spatial analysis is the fuzzing and swapping of coordinate information to protect landowner privacy (USFS 2007). Fuzzing involves artificially introducing errors of up to 1 mile in the geographic coordinates provided for each plot. Further privacy protection is provided by swapping up to 20% of plots on privately owned land parcels with another similar plot in the same county. The definition of “similar” varies by FIA unit but usually includes a measure of forest type, which is based on species composition. Fuzzing and swapping means that localized analyses are unreliable. Ideally, analyses should be restricted to larger regions that span multiple counties, as was done in this study.

Comparability of presettlement and current forest surveys

The HLC and FIA surveys differed in ways that are not completely reconcilable. Quantitative comparison of the two surveys is hampered by two potential biases, which should be properly understood and examined prior to analysis.

On the one hand, there have been concerns about surveyor bias in the selection of bearing trees. Although surveyors may have been biased for or against individual tree taxon, a previous study by Kronenfeld and Wang (2007) showed the effect of taxonomic bias to be small for the HLC data used in this study. We were more concerned with the well-known bias against small bearing trees in the PLSRs (Bourdo 1956), which has led researchers to warn against direct comparison between tree diameters in PLSRs and modern forest inventories (Manies and Mladenoff 2000; Wang 2005). It is unclear how large a tree had to be for it to be considered an acceptable bearing tree, as survey practices were not always consistent from one area to another, and observation of tree diameters was not made for many of the early surveys in the eastern USA (Siccama 1971; Cowell 1995). Diameter cut-offs are important because they affect measures of individual species' occurrence: smaller species will appear less frequent if a larger cut-off is used. Based on available information and assumptions, PLSR studies assessing forest change have assumed cut-offs of 4 in. (Radeloff et al. 1999), 5 in. (Friedman and Reich 2005), and 9 in. (Dyer 2001).

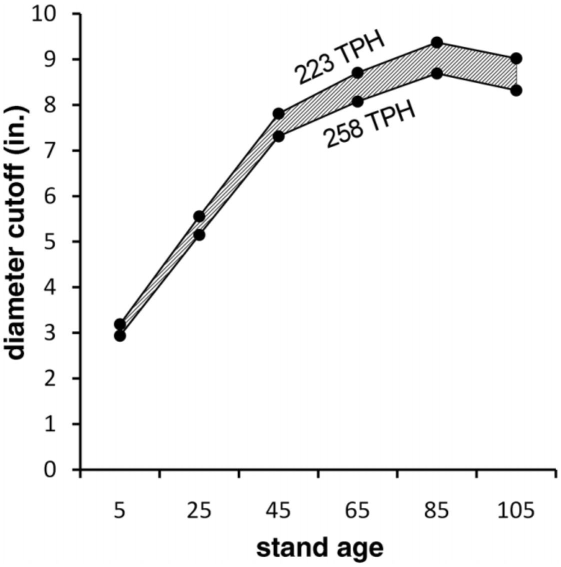
On the other hand, the location of the remnant forests in which the FIA plots were located may be biased toward sites that are relatively inaccessible or have poor soil quality, since forests were less likely to be cleared for agriculture on these sites (Scull and Harman 2004). In contrast, the HLC survey systematically sampled trees as the land was divided into regular townships, and bearing trees were recorded at specific intervals along the survey lines. Analysis needs to be carried out to examine the degree of the potential plot selection bias associated with environmental conditions for the FIA survey before the comparison of the two surveys.

Although unrecorded diameters of bearing trees in PLSRs can never be remeasured, and modern inventories cannot sample where forests are no longer present, these factors must nevertheless be taken into consideration. Below, we detail analyses conducted to assess and minimize the influence of the two potential biases on our comparison.

PLSR tree-size bias

In studies that use GLO records, a plausible diameter cut-off can be determined from the observed distribution of bearing tree diameters, and trees below this cut-off are removed from modern forest inventory data (Friedman and Reich 2005). Such a solution is not available in earlier surveys where tree diameters were not recorded. However, distances from corner post to bearing tree can be used to estimate tree density using standard formulae (Cottam and Curtis 1956; Pollard 1971), which can be used to infer a likely diameter cut-off by comparison with the size and age structure of modern forests. The distance-based density estimation formulae assume a spatially random distribution of trees as well as consistent rule-based tree selection by surveyors, neither of which is likely in PLSRs. However, the effects of these assumptions were modeled in a previous study (Kronenfeld and Wang 2007), and factors to correct for surveyor inconsistencies were developed. Application of these correction factors resulted in density estimates of 223 and 258 TPH for two independent subsets of the HLC survey data.

Fig. 2. Forest Inventory and Analysis diameter cut-offs that would result in densities of 223 and 258 trees per hectare (TPH), for plots grouped by recorded stand age.



The diameter cut-off range that would result in this density of trees in modern FIA plots was determined for each of the six stand-age classes recorded by FIA field workers (Fig. 2). Under the assumption that the presettlement forests were as mature as the oldest FIA stands (approximately 105 years), we estimated conservatively that a diameter cut-off of approximately 9 in. was used by the HLC surveyors. This estimate is based on the assumption of a random spatial pattern. Although aggregation is common in newly regenerated forests, mature forests tend towards dispersal owing to density-dependent mortality (Batista and Maguire 1998). A dispersed tree pattern would cause our estimate of bearing tree density to be too high, and therefore our estimated diameter cut-off to be somewhat lower than the actual cut-off value.

FIA plot selection bias

To examine whether the 261 FIA plots were biased towards certain soil conditions, we used data of soil texture and drainage from the State Soil Geographic (STATSGO) database of the USDA Natural Resources Conservation Service. Texture and drainage are particularly important among various soil properties because they affect the amount of water and nutrients available to tree growth, thereby, determining the potential vegetation of a site (Curtis 1959). We did not use the finely resolved Soil Survey Geographic (SSURGO) database for two reasons. First, the New York SSURGO database does not provide both spatial and attribute data for the study area. Second, even if such data were available, the fuzzing and swapping of FIA plot coordinates means that many FIA plots would be associated with the wrong soil polygon if a finely resolved soil database was used. Thus, the test was performed to detect possible broad-scale bias across the study area but not to assess bias for or against fine-scale soil classes, which were numerous but small in area.

The dominant soil surface texture and drainage for the study area were derived after Wang (2007). Five soil texture classes (loam, very fine sandy loam, silt loam, silt clay loam, and organic soils) and six soil drainage classes (somewhat excessively, well, moderately well, somewhat poorly, poorly, and very poorly drained) were identified. Following Barrett et al. (1995), a 125 m buffer was chosen, and FIA plots within this distance of a soil boundary were eliminated to increase the certainty of locating FIA plots on the correct soil property. Note that some uncertainty still remains because of the fuzzing of FIA plot coordinates; however, any buffer larger than 125 m would have excluded too many plots to allow meaningful analysis. Chi-square tests were conducted to compare the actual frequency of FIA plots in each polygon with the expected frequency to examine whether they were statistically differently distributed across various soil texture and drainage classes. The tests failed to show any statistically significant variation in the density of the FIA plots across the various soil texture and drainage conditions ($P > 0.2$), suggesting that there is no broad-scale soil-related bias in the location of the FIA plots.

Methods for comparing presettlement and present forest conditions

All of the bearing trees in the HLC survey and trees with a dbh ≥9 in. in the FIA survey were analyzed to obtain forest conditions at each time period. In PLSRs, common tree names, which vary from region to region and from surveyor to surveyor, were often used, and collective names such as oak and birch that may indicate more than one species were commonly seen. For these taxonomic ambiguities, we followed the interpretations of Wang (2007).

Changes in relative taxa frequencies

Forest composition at each time period was represented using relative frequencies of taxa, calculated from tree counts of the presettlement HLC and the current FIA surveys in two manners: as tree-based estimates using the percentage of all trees by population count, and as grid-based estimates using the mean of the percentage predicted for each of the grid cells by kriging (see Taxa distribution in the presettlement and the present). The results of these two methods were evaluated for differences. Taxa were categorized as either increasers (more abundant in the FIA than HLC surveys) or decreasers (less abundant in the FIA than the HLC surveys). We use relative frequencies rather than basal areas or other importance value measures because tree counts are available in all PLSRs and can be derived easily from current forest surveys. We note in our analysis of data published by Friedman and Reich (2005) that their relative frequencies of individual trees and of basal areas for 12 species were strongly positively correlated (FIA: Pearson's correlation coefficient $r = 0.89$, $P < 0.001$; PLSR: $r = 0.61$, $P < 0.05$).

Taxa distribution in the presettlement and the present

To increase prediction confidence, spatial distribution patterns were reconstructed for taxa that accounted for ≥1% of trees in both the HLC and the FIA surveys and for taxa whose summed abundance over the two time periods was ≥2%. Reconstructions were also developed for taxa that were not present in one time period but were present in the other at an abundance of ≥1%. This was done to take into account species that had become either essentially extirpated or that had been recently introduced to the study area.

Because the numbers and locations of surveyed sites and trees are different in the HLC and FIA surveys, interpolation methods, such as kriging, that allow the gaps between sample sites to be filled, are desirable. Unlike the average of plots-in-a-polygon method used in prior PLSR research (e.g., Friedman and Reich 2005), kriging takes advantage of spatial autocorrelation in species distributions to predict forest composition in areas that contain few plots, resulting in a continuous estimation surface. Recent PLSR studies have also used kriging and other interpolation methods to reconstruct presettlement vegetation (Manies and Mladenoff 2000; Cogbill et al. 2002; Wang and Larsen 2006). Interpolation allows species distributions to be visualized in continuous representations that enable the comparison of vegetation distribution from data sources with different sampling schemes and between different time periods.

Spatial patterns of taxa distribution in each time period were created using ArcGIS (ESRI Inc., Redlands, California, USA) involving three major steps. First, taxa composition was calculated at each HLC survey post from the corresponding bearing trees and at each FIA plot from inventoried trees with a dbh ≥9 in., multiplied by their respective expansion factors. Second, the semivariogram, representing the relationship between distance separation and data variance, was modeled for each individual taxon by visually fitting an appropriate mathematical function. Third, ordinary kriging was performed separately for each taxon to estimate species abundances at points on a raster grid. Similar to Friedman and Reich (2005), we used a grid size of 6 miles × 6 miles, corresponding to a single township, the basic survey unit of the PLSRs, resulting in 162 grid cells. The use of this coarse resolution also ameliorated concern about the positional accuracy issue of the PLSR and FIA data (Wang 2005).

Changes in spatial patterns

Several methods have been used to represent vegetation change over time in PLSR studies. Often, a series of discrete representations, such as points or polygons, is used to graphically compare the abundance of species or forest types at different points in time (Whitney 1987). Spatially continuous representations present an improvement by providing a more natural illustration of forest change over time (Friedman and Reich 2005) and by allowing quantitative assessment of the area of transition from one forest type to another (White and Mladenoff 1994; Radeloff et al. 1999). In this study, two types of visual portrayals were created to facilitate analysis and provide insights into the changes of abundance for individual tree taxon. First, change maps for individual tree taxa were calculated by subtracting the HLC abundance from the FIA abundance. Second, changes in dominance were assessed by mapping taxa that increased and decreased first- and second-most in each 6 mile × 6 mile cell.

Results

Changes in relative taxa frequencies

More than 40 and 50 tree taxa were recorded in the HLC

Table 1. Comparison of percentage composition of forests in the Holland Land Company (HLC) survey (1790s) and the current Forest Inventory and Analysis (FIA) survey (1990s).

		Tree-based			Grid-based		
HLC taxon	FIA taxon equivalent	HLC	FIA	Δ	HLC	FIA	Δ
Red maple	*Acer rubrum* L.	2.6	11.4	8.8	2.8	11.9	9.1
Sugar maple	*Acer saccharum* Marsh.	21.0	19.2	–1.8	21.2	14.7	–6.5
Yellow birch	*Betula alleghaniensis* Britton.	2.4	1.6	–0.8	2.4	1.2	–1.2
Black birch	*Betula lenta* L.	0.1	0.5	0.4			
Hickory	*Carya* Nutt. sp.	1.1	2.8	1.7	1.2	3.3	2.1
American chestnut	*Castanea dentata* (Marsh.) Borkh.	1.2	*	–1.2	1.1	*	–1.1
Hawthorn	*Crataegus* L. sp.	0.0	0.1	0.1			
American beech	*Fagus grandifolia* Ehrh.	37.0	7.4	–29.6	36.6	5.3	–31.3
Ash	*Fraxinus* sp.	6.0	11.7	5.7	6.0	16.6	10.6
Butternut	*Juglans cinerea* L.	0.3	0.2	–0.2			
Black walnut	*Juglans nigra* L.	0.1	0.3	0.3			
Tamarack	*Larix laricina* (Du Roi) K. Koch	0.3	0.2	–0.1			
Yellow poplar	*Liriodendron tulipifera* L.	0.1	0.4	0.3			
Cucumber	*Magnolia acuminata* (L.) L.	0.6	0.3	–0.4			
Domestic apple	*Malus sylvestris* (L.) Mill.	*	1.0	1.0	*	1.9	1.9
Ironwood	*Ostrya virginiana* (Mill.) K. Koch	1.2	0.7	–0.5			
White pine	*Pinus strobus* L.	2.0	3.1	1.0	2.4	1.6	–0.8
Scots pine	*Pinus sylvestris* L.	*	1.1	1.1	*	1.4	1.4
Sycamore	*Platanus occidentalis* L.	0.3	0.1	–0.2			
Poplar, aspen	*Populus* sp.	0.5	6.5	6.1	0.5	9.6	9.1
Black cherry	*Prunus serotina* Ehrh.	0.5	7.9	7.4	0.4	9.3	8.9
White oak	*Quercus alba* L.	3.0	1.2	–1.8	2.7	1.4	–1.3
Swamp white oak	*Quercus bicolor* Willd.	0.0	0.1	0.1			
Chestnut oak	*Quercus prinus* L.	0.1	0.1	0.1			
Red oak	*Quercus rubra* L.	0.1	6.8	6.7	0.2	3.9	3.7
Black oak	*Quercus velutina* Lam.	1.1	0.0	–1.1			
Black willow	*Salix nigra*	0.1	1.3	1.3			
American basswood	*Tilia americana* L.	5.1	2.1	–3.0	4.9	2.1	–2.8
Eastern hemlock	*Tsuga canadensis* (L.) Carrière	8.3	7.8	–0.6	8.3	5.0	–3.3
Elm	*Ulmus* sp.	4.6	1.5	–3.1	4.3	3.3	–1.0
Total		99.7	97.4		95.0	92.5	

Note: A value of 0.0 indicates a trace (<0.05%), while the asterisk (*) indicates no occurrence. Tree-based estimates are percentages of all trees; grid-based estimates are means of the percentage of that taxon in each of the 162 grid cells. Change (Δ) is calculated as the FIA value minus the HLC value. Values to one decimal place were used for presentation but not for calculation.

and FIA surveys, respectively. About 96% of the FIA trees were recorded to the species level. Some species were grouped to the genus level because collective tree names that may indicate more than one species were often used in PLSRs. In addition, HLC bearing trees that were marked as saplings were removed. These comprised a very small fraction of the HLC bearing tree database (<0.1%); hence, their removal would not cause significant changes in forest composition. Taxa in the HLC survey that had equivalents in the FIA are listed in Table 1, and they comprised, respectively, 99.7% and 97.4% of the trees in the two surveys. Unknown species comprised <0.1% of the HLC trees and 0.2% of the FIA trees.

In the presettlement era, American beech was the most abundant tree species at 37.0%, followed by sugar maple at 21.0%, eastern hemlock (*Tsuga canadensis* (L.) Carrière) at 8.3%, the genus ash (*Fraxinus* sp.) at 6.0%, and American basswood (*Tilia americana* L.) at 5.1% (Table 1). In the current era, sugar maple is the most abundant species at 19.2%, followed by the genus ash at 11.7%, red maple (*Acer rubrum* L.) at 11.4%, black cherry (*Prunus serotina* Ehrh.) at 7.9%, and eastern hemlock at 7.8%. Other taxa that exceed 5% of the present forest composition include red oak (*Quercus rubra* L.) at 6.8% and the genus poplar (*Populus* sp.) at 6.5%. Grid-based estimates of abundance derived from kriging (Table 1) are essentially identical to the tree-based estimates for the HLC ($r = 1.00$, $P < 0.001$) and very similar to the tree-based estimates for the FIA ($r = 0.89$, $P < 0.001$). In the presettlement forest, the two most abundant species together made up 58.0% of the trees and 57.8% of the grid-based landscape, while in the current forest it took the five most abundant species together to make up 58.0% of the trees and 62.1% of the grid-based landscape.

The taxa with the five largest increases in tree-based estimates from the presettlement to the present were red maple (8.8%), black cherry (7.4%), red oak (6.7%), poplar (6.1%), and ash (5.7%), and the taxa with the five largest decreases were beech (–29.6%), elm (*Ulmus* sp., –3.1%), basswood (–3.0%), sugar maple (–1.8%), and white oak (–1.8%) (Table 1). Beech encounters the most dramatic percentage change. No other taxon decreased its share of the proportional abundance by more than 5%. The grid-based estimates provide a slightly different set and sequence of taxa: the five largest increasers were ash, red maple, poplar, black cherry, red oak; and the five largest decreasers were beech, sugar maple, hemlock, basswood, and white oak. The tree-based and grid-based estimates of change are, however, highly correlated (r = 0.97, P < 0.001).

For taxa that comprised small proportions of the trees, American chestnut (*Castanea dentata* (Marsh.) Borkh) has disappeared during this time period (Table 1). Alder (*Alnus incana*), balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), and white cedar (*Thuja occidentalis* L.), each constituting ≤0.1% of the presettlement vegetation (cf. Wang 2007), were not seen in the present forest landscape. Introduced taxa, such as tree of heaven (*Ailanthus altissima* (Mill.) Swingle), introduced larch (most likely *Larix decidua* Mill.), osage orange (*Maclura pomifera* (Raf.) C.K. Schneid.), apple (*Malus* sp.), Norway spruce (*Picea abies* (L.) Karst.), and Scots pine (*Pinus sylvestris* L.), have gained a foothold in the current forests. They collectively account for 3.9% of the composition (data not shown).

Spatial distribution change

Comparison of the distributions of different taxa

Spatial patterns of distribution were reconstructed for 17 taxa whose relative frequencies met the criteria specified in the section Taxa distribution in the presettlement and the present, including all five of the taxa that increased the greatest and the five taxa that decreased the greatest from both tree-based and grid-based estimates. Presettlement and present distributions and spatial patterns of change for selected taxa are shown in Fig. 3. The major decreasers exhibit unique patterns of presence and change (Fig. 3*a*). Beech, formerly abundant everywhere except for where elm dominated, decreased throughout its range. Sugar maple, formerly abundant throughout much of the study area, decreased in the northern Erie–Ontario Lowland and in the east–central portion of the study area but increased to the south and west of this region. Elm maintained its greatest abundances in the Erie–Ontario Lowland, and exhibited interdigitated patches of increase and decrease throughout most of the study area. White oak maintained its disjunct distribution, with peak abundances in the north and south, but decreased in the cells in which it was most abundant and increased in adjacent cells. Hemlock is illustrated because although its abundance did not decrease much, its core area of distribution shifted markedly, decreasing primarily in the areas of its peak abundance and increasing in the zone between those areas of former maximal abundance.

The major increasers also show unique patterns of presence and change (Fig. 3*b*). Most of the cells now contain taxa that did not dominate anywhere in the presettlement era. Red maple maintains its two centers of maximal abundance in the northwest and south and increases throughout the study area. Black cherry, red oak, and poplar were not abundant in any areas in the presettlement era but increased in different parts of it in the current era: black cherry increased everywhere but mostly in the southwest; red oak increased disjunctively in the north and south, but not in the center; and poplar increased everywhere but mostly in the Erie–Ontario Lowland in the north. Ash was formerly most abundant in the Erie–Ontario Lowland but in the present-day survey it increased mostly in the northeastern part of the study area where red maple is not dominant.

Maximum increasers and decreasers

Maps of the highest and second highest increaser and decreaser in each of the 162 cells (Fig. 4) complement the above-described patterns. A total of six taxa exhibited the greatest decrease in at least one cell (Fig. 4*a*), with beech being that major decreaser in close to 80% of the cells (Table 2). In contrast, 10 taxa exhibited the greatest increase in at least one cell, with no single taxon standing out (Fig. 4*c*).

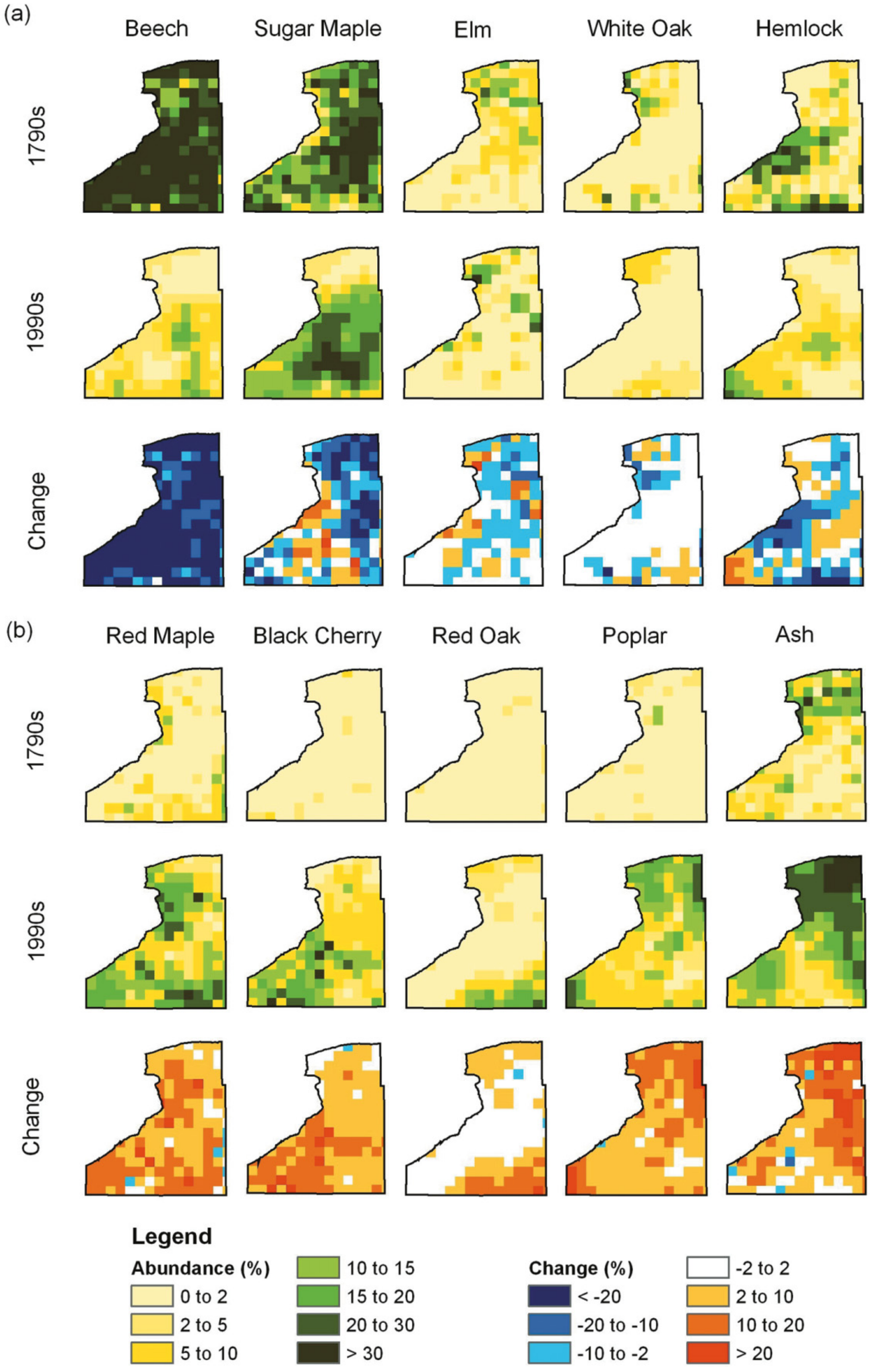
The spatial pattern for the greatest decreasers is essentially that of beech declining everywhere (Fig. 4*a*). Cells with sugar maple as the greatest decreaser often had beech as the second greatest decreaser (Figs. 4*a* and 4*b*). The pattern is more heterogeneous for the second greatest decreasers: the decrease of (*i*) hemlock in a large cluster along Lake Erie, (*ii*) of white oak and of elm in small clusters, in the western and the northern parts, respectively, of the lowland area, and (*iii*) of chestnut and white pine (*P. strobus*) in the southern part of the upland (Fig. 4*b*). The spatially extensive decrease of presettlement beech was supplanted by many early successional taxa (Fig. 4*c*); more than 30% and 20% of the study area had ash and black cherry, respectively, as the greatest increasers (Table 2). For the second greatest increasers, the pattern is basically poplar in the north lowland area, red maple in the southwest, and red oak in the southeast upland area. The nonnative taxa, Scots pine and apple, were the second greatest increasers in only a small area (Fig. 4*d*), within which beech and basswood lost high proportional abundance (Figs. 4*a* and 4*b*).

Discussion

Changes in relative taxa frequencies

The results of this study are consistent with prior work in the northeastern USA, where beech and sugar maple were dominant (Siccama 1971; Seischab 1990; Marks and Gardescu 1992) and hemlock was a large component of the presettlement forests (Cogbill et al. 2002). Significant changes in forest composition from presettlement to the present are consistent with most other regions of the northeastern USA in that a large decrease in beech was detected (Whitney and DeCant 2003). Beech has decreased from 37.0% to 7.4% of the trees, a shift from being the first- to sixth-most abundant taxa. A decrease in white oak following European settlement was also observed in the northeastern USA, especially in areas where the species was previously most prominent (Dyer 2001). The relative abundance of sugar maple dropped from 21.0% to 19.2% (Table 1). The simulation result of Kronenfeld and Wang (2007) suggests that there may have been a bias towards sugar maple in the HLC surveys, so that the actual percentage would more likely have been between 14.2% and 18.0%. Regardless of the exact value, sugar maple still shifted from being the second to being the most abundant species. As the new dominant species, sugar maple has an abundance of only 52% of that of the former dominant species, beech, in the presettlement landscape of the study area.

Fig. 3. Distribution patterns and change maps of (*a*) five selected taxa with decreased frequencies and (*b*) five taxa with the greatest increase in frequency, between presettlement (1790s) and present (1990s), in 6 miles × 6 miles grid cells. The range from –2% to 2% is used to show areas of minimum change, rather than a value of 0% indicating no change, to account for uncertainty in predictions.



Although Friedman and Reich (2005) suggested that tree-size-related bias in the PLSRs would likely have had minimal impacts on comparing the regional patterns of change, we found that forest composition would be different when different diameter cut-offs are used for the FIA data (Table A1). For example, if no cut-off is applied, red oak would have been excluded from the analysis of spatial patterns of change; hawthorn (*Crataegus* L. sp.) would have become

Fig. 4. Tree taxa that increased and decreased the greatest and second greatest within each 6 miles × 6 miles cell. Seventeen taxa were analyzed, among which three of the taxa were recorded in only one time period: chestnut in the presettlement, and Scots pine and apple in the present. Only 16 taxa are mapped because, although hickory was included in the analysis, it was not the first or second greatest increasing or decreasing taxon in any cell. Hemlock, sugar maple, elm, and ash were increasers in some cells and decreasers in others.

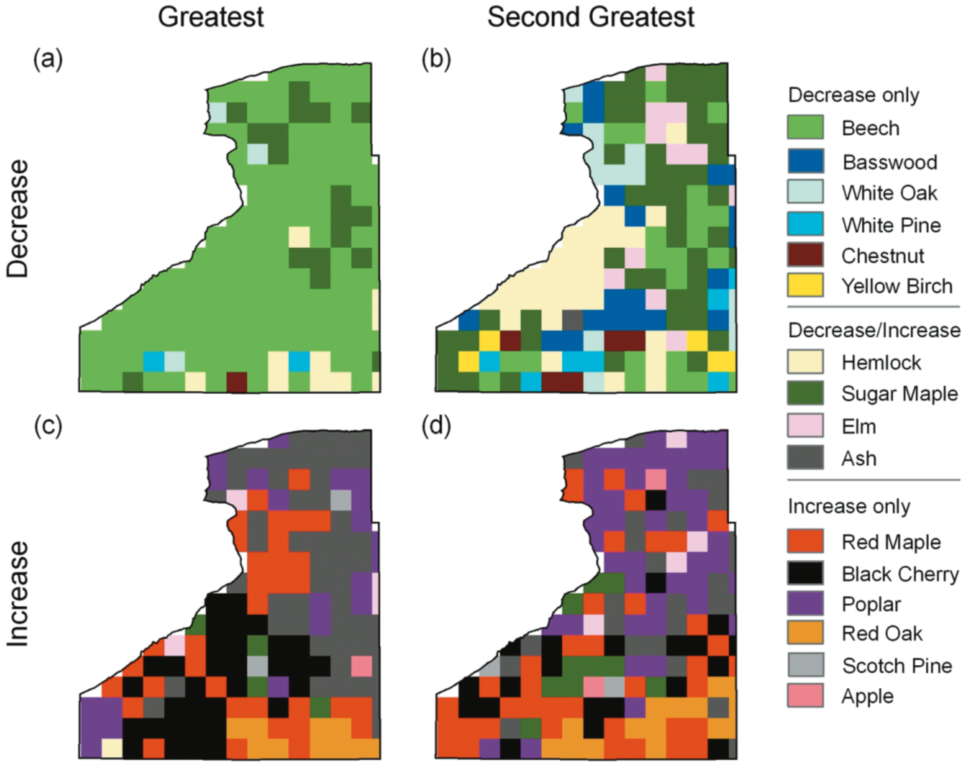


Table 2. The percentage of grid cells in which a tree taxon exhibited the greatest and second greatest decreases and increases in relative abundance.

	Decreasing (%)		Increasing (%)	
Taxon	Greatest	Second greatest	Greatest	Second greatest
Beech	79.0	14.2		
Basswood		12.3		
White oak	1.9	7.4		
White pine	1.2	4.3		
Chestnut	0.6	3.1		
Yellow birch		3.1		
Hemlock	6.2	17.9	0.6	
Sugar maple	11.1	30.2	2.5	6.2
Elm		6.8	2.5	2.5
Ash		0.6	32.1	16.0
Red maple			21.0	24.1
Black cherry			20.4	13.0
Poplar			13.0	26.5
Red oak			6.2	9.3
Scots pine			1.2	1.2
Apple			0.6	1.2
Total	100.0	100.0	100.0	100.0

the taxon that increased the most, rather than red maple; and ironwood (*Ostrya virginiana*) would have shown an increasing trend rather than decreasing. A higher cut-off such as 4 in. dbh would have a similar effect but less pronounced. Although we agree with previous researchers that general conclusions regarding forest change are not invalidated by a lack of knowledge of diameter cut-offs, nevertheless careful analysis of surveyor selection criteria will greatly increase the level of confidence in such conclusions.

Spatially resolved comparison

Our approach is to use interpolated spatial patterns as the basis of examining forest change between the PLSR and FIA surveys. The spatial approach is useful as a means of comparing data of different time periods, which often have different sampling schemes and various quality issues. In our analysis, the tree-based and grid-based estimates resulted in slight differences in the predicted amount of increase or decrease (Table 1). These differences do not drastically change the results of our analyses, but they do highlight two different conceptualizations of the forest. Since forested FIA plots are dispersed across the landscape in proportion to actual forests, the tree-based estimates best reflect actual species abundances. In contrast, the grid-based estimates that we used represent potential abundances if the entire landscape were forested. Although actual abundances are valid for inventories of forest resources and biodiversity, potential abundances are arguably more significant for identifying long-term ecological processes.

The spatial approach is also useful as a representation tool, allowing visualization of forest change at both the level of the individual taxon distribution and of the overall forest landscape. At the individual taxon distribution level, our spatially resolved comparison characterizes patterns of change that can not be seen from summary tables, a common and often the only approach to show forest change in prior PLSR studies (Jackson et al. 2000; Leahy and Pregitzer 2003). For example, of the five decreasers mapped, only beech does not have cells in which it also increased; of the five increasers mapped, all have cells in which they also decrease. In addition, the overall frequencies of sugar maple and hemlock suggest that their abundances were stable during this time period (Table 1), but their distributional patterns and change maps speak a different story, showing that their areas of maximal abundance have shifted toward the southwest (Fig. 3*a*). At the overall forest landscape level, maps of maximum increasers and decreasers summarize the patterns of change from 17 taxa (Figs. 4*a*–4*d*). Change maps provide added value by illustrating spatial relationships between decreasing and increasing taxa. For example, the spatial patterns of the increasers (Figs. 4*c* and 4*d*) suggest that the spatially extensive decrease of beech (Fig. 4*a*) was replaced by ash and poplar in the north lowland area, red maple and black cherry in the southwest, and red oak in the southeast upland area.

Just as with all the other historical ecological methods, uncertainties remain with respect to the estimations of the presettlement and present forest landscapes and their changes over time. There may be two issues related to spatial uncertainties. First, methods of spatial distribution reconstructions, such as kriging used in this study, provide less confident predictions for taxa with small sample sizes. To alleviate this potential issue, this study and other PLSR studies have limited analyses to taxa with at least 1% or 2% of the total tree database (He et al. 2000; Dyer 2001; Wang 2007). The exclusion of taxa with small but locally important proportions would have little impact on broad patterns of forest composition but may result in an underestimation of the diversity of the forest landscape. Second, the presence of areas with sparse observations may influence the confidence of spatial prediction. This issue can be discussed at two levels: the variations within the FIA dataset and the differences between the HLC and FIA datasets. Within the FIA dataset, the kriging process weighted individual plots more strongly and resulted in lower certainty levels in the sparsely sampled Erie–Ontario Lowland than in the more densely sampled Appalachian Upland. The different FIA sampling densities in the two physiographic regions might also explain the lower correlation coefficient between the grid-based and tree-based estimates for the FIA data ($r = 0.89$) than that for the HLC data ($r = 1.00$). Despite this, both correlation coefficients are statistically significant ($P < 0.001$), supporting the use of grid estimates in the analysis.

Between the HLC and FIA datasets, differences in the density of sampling locations and number of trees recorded at each location may influence the spatial structure of interpolated taxon distribution patterns. When the same number of sample points is used to estimate taxon abundances at an unsampled location, FIA plots will be pulled in from farther away and include a greater number of trees than HLC plots. This may be the reason why the current distributions of sugar maple and ash appear smoother than the presettlement distributions of the same taxa (Fig. 3). Before conducting our final analysis, we tested different numbers of points to be included for the interpolation and for the subsequent conversion into grid. The resulting patterns showed slight differences, but when converted into the coarse resolution 6 miles × 6 miles, the general trend of forest change remained similar. It should be recognized that uncertainties remain with regard to the predictions of taxa occurrence, especially at the level of the individual grid cell. However, this should not be a major issue that would alter the general trend of change illustrated in this study because the spatial patterns examined are across multiple grid cells.

Researchers should also be reminded of two possible temporal uncertainties. First, presettlement vegetation reconstructed from the PLSRs does not represent a landscape entirely free from human alternation, and disturbances by Native Americans have been noted in some PLSRs (Marks and Gardescu 1992). However, the PLSRs represent vegetation that developed under a regime of human–landscape interaction very different from that which followed major European settlement and, as such, provide a useful reference for evaluating human influences. Second, although some studies have argued that steady-state communities dominated the presettlement northern hardwood forest landscape (Bormann and Likens 1979; Seischab and Orwig 1991), in fact both the presettlement and the present forest ecosystems were not at all static. It must be remembered that most vegetation change studies involve only two points in time, and so the results do not provide complete information on the temporal dynamic of the forest landscape.

Possible causes for the forest landscape change

Spatially resolved comparisons allow possible causal explanations to be drawn from the spatial patterns of change. The most likely factors contributing to the changing composition and distribution of western New York forests since presettlement are related to human influences. Anthropogenic incursion into the forest landscape has been primarily through the direct agent of disturbance through forest clearing. Much of the region, especially the Erie–Ontario Lowland, was converted into cropland or pasture before recently reverting to forest. As a result, beech, a late successional species thriving in the low-light environments of mature forests, has decreased the most (Table 1, Fig. 3*a*). Conversely, early successional species, such as black cherry, red maple, and white ash (*Fraxinus americana* L.), are old field invaders capable of seeding into grass sod (Whitney and Somerlot 1985) and have increased dramatically (Fig. 3*b*). Based on the FIA data, note that most of the ash now is white ash, accounting for 9.8% of the current forests (data not shown). The general decrease of late successional species and the increase of early successional species are consistent with one of the distinctive changes noted in other northern hardwood forests in prior studies (Dyer 2001; Whitney and DeCant 2003).

The issue of to what extent and in what period did the Native Americans influence the historical landscape has been an area of debate (Guyette et al. 2002). Natives of this region cleared forests to build villages and to obtained fuelwood and burned forests to clear land for corn agriculture and to open forests to increase forage for game (Whitney 1996). Native burning has been attributed to the presettlement white oak dominance (Black et al. 2006), and indeed this species was observed most in the northwestern part of the study area (Fig. 3*a*) where Indian reservations were located (Tuscarora Reserve and Buffalo Creek Reserve) (cf. Wang 2007, p. 502). The collapse of native societies and population sizes in the Great Lakes region between 1650 and 1800 would have reduced the amount of native clearance and burning (White 1991). Indeed, a large decrease of white oak observed for the grid cells close to the Indian reserves (Figs. 4*a* and 4*b*) may reflect the loss of native burning, although selective cutting for railroad and a variety of construction work might also have contributed to its decrease (Whitney and Somerlot 1985). The lack of early successional tree species in the HLC survey suggests that the Native American population may have collapsed early, allowing time for late successional beech and sugar maple to dominate prior to the time of the survey. Alternatively, it may indicate that native burning and clearance, though present, was not extensive in this region.

Disease has influenced a number of tree species in the northeastern USA presettlement forest. Dutch elm disease, first noted in Ohio in 1930, could be an important factor for the decrease of elm from 4.6% to 1.5% (Table 1). The introduced chestnut blight to the United States in the first decade of the 20th century resulted in the decrease of American chestnut from 1.2% in the presettlement to nonexistent in the FIA survey (Table 1). It has been suggested that most of the sites formerly occupied by chestnut would be taken over by oaks, maples, and other species that were associated with chestnut (Hepting 1974), and we do see that areas with large decreases in chestnut exhibit large increases in red maple or red oak (Fig. 4).

Although it is easy to attribute observed changes to a single cause, forest composition dynamics in recent centuries are regionally variable and subtle, involving many interacting and interdependent factors. For example, beech bark disease was evident throughout New York State by 1975, affecting beech growth in many areas in the northeastern USA (Houston 1994). Pollen records from the northeastern USA, however, show that beech had decreased markedly prior to the arrival of beech bark disease (Fuller et al. 1998), suggesting that it has probably only added to the decrease and perhaps held its regrowth in check.

Some pollen studies in the northeastern USA during the late Holocene, specifically during the Little Ice Age, have also suggested that climate contributed to the prehistoric decrease in beech and hemlock (Gajewski 1987; Jacobson and Davis 1988). Conversely, other pollen diagrams (Russell et al. 1993; Fuller et al. 1998) reveal the effects of European settlement and subsequent land use on forest changes from prehistoric time to the present, a time period more relevant to this study. Forest changes derived from the PLSR and FIA surveys in this study seem to suggest a slight tendency towards an increase in southern species and a decrease in northern species (Table 1, Fig. 3). To verify this observation, the species distributions of Little (1971) were compared with USDA plant hardiness zones (Cathey 1990) to identify taxa with ranges centered north or south of the study region. Of eight taxa with clearly southern centers, five increased in abundance (black birch (*Betula lenta* L.), hickory (*Carya* Nutt. sp.), yellow poplar (*Liriodendron tulipifera* L.), black cherry, and chestnut oak (*Quercus prinus* L.)), and three decreased (cucumber (*Magnolia acuminata* L.), white oak, and black oak (*Quercus velutina* Lam.)). Of four clearly northern species, one increased in abundance (white pine) and three decreased (sugar maple, butternut (*Juglans cinerea* L.), and tamarack (*Larix laricina* (Du Roi) K. Koch)). Among rare species, two northern species present in the HLC (black spruce, white cedar) were not found in the FIA data. Although these results are consistent with climatic warming, they are statistically inconclusive and confounded by the effects of land use change and disease on many of the individual taxa. A more rigorous test of climatic influence would require observation over a wider geographic region to compare changes that have occurred in different parts of each taxon's range.

Insights into spatial patterns of forest landscape change provide one powerful means for further studies on hypothesis testing of causation because different possible factors would have different spatial signatures. For example, if succession is the major cause for beech decrease, then areas of old-growth forest should still have high beech abundance, which seems to be the case. The remaining patches of beech abundance are located in interior areas where mature forests are more common, while along both lake shorelines beech has declined. Beech bark disease, on the other hand, would be likely to hit hardest in areas of former dominance. In contrast to the former widespread dominance of beech, the spatial segregation of dominance among the increasers likely reflects a combination of environmental factors and human land use practices. Red maple and black cherry have increased most in the Appalachian Upland (Fig. 3*b*), perhaps related to their favoring of slightly more precipitation and lower pH soils (Prasad and Iverson 1999-ongoing) than poplar or ash. White ash's dominance in the Erie–Ontario Lowland is likely due to the more calcareous and clay rich nature of the soils in this region (Burns and Barbara, 1990).

Inferences here have been made based on visual observation of spatial distributions and patterns of change. The results demonstrate value in spatially explicit data analysis, and suggest avenues for further research using geographical hypotheses to determine causal mechanisms of forest compositional change. As noted above, more rigorous testing of climatic hypotheses would require analysis over broader geographic regions to compare opposite sides of a taxon's distribution along broad environmental gradients. Evaluation of the role of soils, topography and other local environmental factors would require modeling that employs detailed geographic information system coverages of environmental data and the spatial patterns of forest landscape change derived from, for example, our spatially resolved comparisons. Both types of analysis must be undertaken with caution, considering the appropriate resolution of analysis, possible biases in data sources, and competing causal explanations.

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Appendix 1.

Table A1. Comparison of percent composition of forests in the presettlement Holland Land Company (HLC) survey (1790s) and the current Forest Inventory and Analysis (FIA) survey (1990s) using diameter cut-offs at 0, 4, and 9 inches.

			FIA (%)			Δ (%)		
HLC taxon	FIA taxon equivalent	HLC (%)	0 in.	4 in.	9 in.	0 in.	4 in.	9 in.
Red maple	*Acer rubrum* L.	2.6	10.8	12.7	11.4	8.2	10.1	8.8
Sugar maple	*Acer saccharum* Marsh.	21.0	17.3	16.6	19.2	–3.7	–4.5	–1.8
Yellow birch	*Betula alleghaniensis* Britton.	2.4	1.5	1.8	1.6	–1.0	–0.7	–0.8
Black birch	*Betula lenta* L.	0.1	0.4	1.0	0.5	0.3	0.9	0.4
Hickory	*Carya* Nutt. sp.	1.1	1.1	1.8	2.8	0.0	0.7	1.7
American chestnut	*Castanea dentata* (Marsh.) Borkh.	1.2	*	*	*	–1.2	–1.2	–1.2
Hawthorn	*Crataegus* L. sp.	0.0	9.5	2.6	0.1	9.5	2.6	0.1
American beech	*Fagus grandifolia* Ehrh.	37.0	6.8	5.2	7.4	–30.2	–31.8	–29.6
Ash	*Fraxinus* sp.	6.0	11.1	12.7	11.7	5.1	6.7	5.7
Butternut	*Juglans cinerea* L.	0.3	0.0	0.1	0.2	–0.3	–0.3	–0.2
Black walnut	*Juglans nigra* L.	0.1	0.1	0.3	0.3	0.0	0.2	0.3
Tamarack	*Larix laricina* (Du Roi) K. Koch	0.3	0.1	0.3	0.2	–0.2	0.0	–0.1
Yellow poplar	*Liriodendron tulipifera* L.	0.1	0.1	0.2	0.4	0.0	0.1	0.3
Cucumber	*Magnolia acuminata* (L.) L.	0.6	0.2	0.1	0.3	–0.5	–0.5	–0.4
Domestic apple	*Malus sylvestris* (L.) Mill.	*	6.3	4.3	1.0	6.3	4.3	1.0
Ironwood	*Ostrya virginiana* (Mill.) K. Koch	1.2	2.5	2.5	0.7	1.3	1.3	–0.5
White pine	*Pinus strobus* L.	2.0	0.5	1.5	3.1	–1.5	–0.6	1.0
Scots pine	*Pinus sylvestris* L.	*	0.5	1.2	1.1	0.5	1.2	1.1
Sycamore	*Platanus occidentalis* L.	0.3	0.0	0.0	0.1	–0.3	–0.2	–0.2
Poplar, aspen	*Populus* sp.	0.5	4.4	7.1	6.5	3.9	6.6	6.1
Black cherry	*Prunus serotina* Ehrh.	0.5	5.4	5.7	7.9	5.0	5.2	7.4
White oak	*Quercus alba* L.	3.0	0.5	0.6	1.2	–2.4	–2.3	–1.8
Swamp white oak	*Quercus bicolor* Willd.	0.0	0.0	0.1	0.1	0.0	0.1	0.1
Chestnut oak	*Quercus prinus* L.	0.1	0.0	0.1	0.1	0.0	0.0	0.1
Red oak	*Quercus rubra* L.	0.1	1.4	3.3	6.8	1.3	3.2	6.7
Black oak	*Quercus velutina* Lam.	1.1	0.1	0.1	0.0	–1.0	–1.0	–1.1
Black willow	*Salix nigra*	0.1	0.7	0.7	1.3	0.6	0.6	1.3
American basswood	*Tilia americana* L.	5.1	0.8	1.5	2.1	–4.3	–3.6	–3.0
Eastern hemlock	*Tsuga canadensis* (L.) Carrière	8.3	3.6	6.9	7.8	–4.7	–1.4	–0.6
Elm	*Ulmus* sp.	4.6	3.4	3.6	1.5	–1.1	–0.9	–3.1
Total		99.7	89.3	94.4	97.4	–17.3	–10.9	–3.4

Note: A value of 0.0 indicates a trace (<0.05%), while the asterisk (*) indicates no occurrence. The cut-off of 0 in. means that all trees in the FIA survey were included. Change (Δ) is calculated as the FIA value minus the HLC value. Values to one decimal place were used for presentation, but not for calculation.