

Effects of clearance and fragmentation on forest compositional change and recovery after 200 years in western New York

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Abstract This study investigated the effects of widespread forest clearance and fragmentation on forest compositional change between pre-settlement and the present (ca. 1800–1993) in western New York. Forest compositional turnover metrics were calculated to evaluate whether soil conditions accounted for the forest compositional change, to investigate how forest clearance might have contributed to the change, and to compare with the amount of change noted in other studies that compared the pre-settlement land surveys and the current Forest Inventory and Analysis (FIA) surveys. The results suggested weak relations between the forest compositional change and soil conditions. The amount of change at the county level was positively correlated with the amount of forest clearance by the late 1800s and negatively correlated with the amount of remnant forest in the late 1800s. Furthermore, while the geographic distributions of

late-successional taxa in the study area exhibited increased patchiness and decreased contagion, those of early-successional taxa exhibited decreased patchiness and increased contagion. Comparison of taxa's changed abundances with seven life history characteristics commonly associated with early- and late-successional status showed that taxa's changed abundances were significantly related to maximum life and shade tolerance. Analysis of different-sized trees in different ages in the FIA survey indicated the possibility of the current forests trending back toward their pre-settlement composition.

Keywords Succession · Fragmentation · Landscape change · Forest Inventory and Analysis · Pre-settlement vegetation · Western New York

Introduction

Widespread forest clearance results in many changes to the physical and ecological characteristics of a forested area (Lindenmayer and Fischer 2006). Three changes among others are often identified. First, forest clearance typically fragments the forest into smaller and more isolated patches with fewer floral and faunal species (Crawley and Harral 2001), the number of which decreases with the decreased size and increased isolation of the remnant patch (Ferraz et al. 2007). Second, the species that remain in those remnant patches have different life history characteristics than

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those in the pre-disturbance forest (Montoya et al. 2008). Third, forest clearance typically fragments not only just the forest, but also the geographic distribution of a species (Fahrig 2003). Reforestation should, in theory, reverse the changes created by forest clearance (Quine and Watts 2009). Return of the forests to the pre-disturbance state may be slowed, however, because of the time required for propagule dispersal and for successional changes in the forest stand environment (Lindborg and Eriksson 2004).

The northeastern United States provides an interesting location to explore how forests can change in response to widespread forest clearance and fragmentation that is followed by natural reforestation (as opposed to active planting) and forest agglomeration (Whitney 1996). Pollen records from lake sediments show that anthropogenic disturbance of forests in the northeastern USA has decreased the abundance of late-successional species and increased the abundance of early-successional species (Russell et al. 1993), and that, despite regional natural reforestation, forests are not returning to their pre-European settlement composition (Fuller et al. 1998). Similar results have been found in comparisons of the Forest Inventory and Analysis (FIA) surveys of present forests by the US Department of Agriculture (USDA) Forest Service with Pre-settlement Land Survey Records (PLSRs) (Dyer 2001; Whitney and DeCant 2003; Friedman and Reich 2005). Recent analysis at the broad northern Great Lakes region level also documents a shift in species dominance and an increase in homogeneity (Schulte et al. 2007). Soil characteristics have been found to influence land-cover changes since the pre-settlement (Rhemtulla et al. 2007). It is possible, however, that comparisons between pre-settlement and present forests may be biased since existing forest patches, such as surveyed by the FIA, can be concentrated on agriculturally inferior soils that are either coarse-textured or poorly drained (Scull and Harman 2004).

In this article, we use PLSR and FIA surveys from western New York to help further our understanding of how and why forests in the northeastern USA have changed in response to widespread forest clearance and the likely attendant fragmentation between pre-settlement and present. In a previous study (i.e., Wang et al. 2009), we examined the comparability of the two surveys of western New York by applying correction factors to the PLSR survey to minimize its

tree-size bias and evaluating the degree of FIA plot selection bias associated with environmental conditions. We also assessed the use of geostatistics to create comparable, spatially resolved coverages from the PLSR and FIA data points, and discovered which tree taxa had increased and which had decreased in abundance. In this article, we analyze factors that may have influenced the degree to which different taxa increased and decreased in abundance. Specifically, we address four questions. First, do the tree species that increase in abundance between pre-settlement and present have statistically significant differences in life history characteristics from the species that decrease in abundance? Second, do the forests of the pre-settlement and the naturally reforested forests of the present differ more in areas that experienced greater amounts of forest clearance and how are the differences in the amount of forest clearance associated with soil conditions? Third, did the geographic distributions of each of the individual tree species that decreased in abundance become more fragmented and, of those that increased in abundance become more agglomerated? Fourth, relative to young forests, do older forests have relative abundances of tree species in the understory that are more similar to those of the pre-settlement forest?

Materials and methods

Study area

The study area is the Holland Land Company (HLC) purchase of western New York (from 42°N to 43°23'N and 78°5'W to 79°45'W) (Fig. 1). Its northern part belongs to the Erie-Ontario Lowland, a region of low relief dominated by lacustrine deposits; the southern part is the Appalachian Upland, glaciated except for the Allegheny Hills subdivision (Thompson 1977). Mean annual temperature is about 8.3°C and mean annual precipitation ranges from 800 to 1120 mm (Easterling et al. 1996).

The study area consists of four full and four partial counties (Fig. 1). Census records of population size from the Minnesota Population Center (MPC 2004) are available for each county beginning in the early- to mid-1800s. These records show that population has changed little for the five least-populated counties since the mid-1800s.

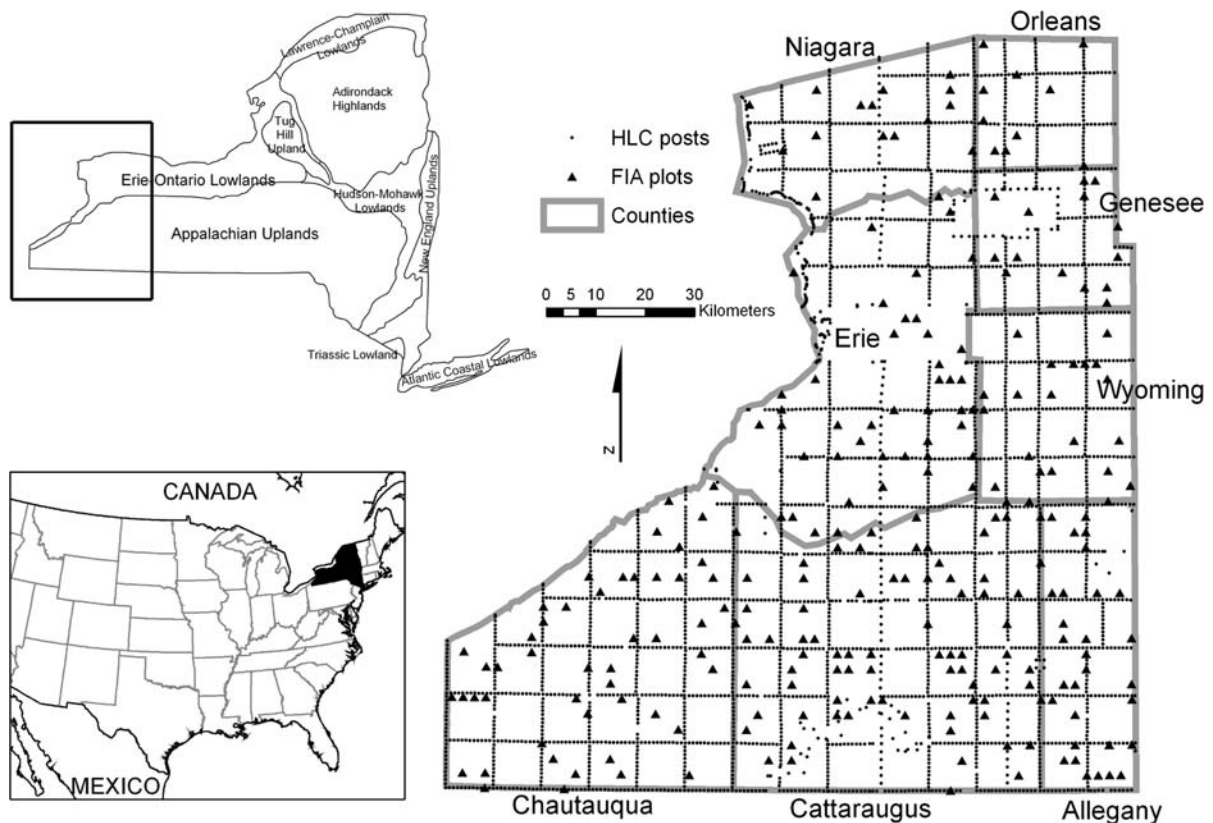


Fig. 1 The study area of the Holland Land Company (HLC) purchase in western New York. It consists of four full (Niagara, Erie, Chautauqua, and Cattaraugus) and four partial (Orleans,

Genesee, Wyoming, and Allegany) counties (modified from Wang et al. 2009, p. 78)

The census records also provide information on forest clearance regarding the area in each county that was farmland (MPC 2004). Farmland was categorized as improved (tilled, fallow, pasture or orchard), unimproved (owned by a farmer but not improved, and typically woodland, abandoned field or swamp), or total (improved plus unimproved) (Table 1). Decadal data were available on the area of unimproved farmland from 1860 to 1890 (except 1870) and on the area of improved farmland from 1860 to 1920 (except 1910). Data on the total area of farmland were available for 1900, 1920, 1930, and 1950 and were calculated for 1860–1890 by summing the areas of improved and unimproved farmland. In each of the eight counties, the area of unimproved land steadily decreased between 1860 and 1890, and was between 8 and 24% in 1890. The area in improved farmland peaked in 1880 in six of the eight counties and was between 52 and 81% in 1890. Total

farmland peaked in all counties in 1880 and then declined steadily to 1950. That the peak in total farmland in Wyoming County in 1880 was 109% of the area of Wyoming County suggests that there could be either errors in the estimates of farm acreage that the farmers provided to the Census, confusion over changed definitions of improved and unimproved farmland, or changes in the area of a county between censuses. Consequently, we converted the acreages into percentages.

The decrease in area of farmland beginning in 1880 occurred through much of the northeastern USA due to urbanization and the lure of farmland in the American Midwest (Whitney 1996). In 1880, the acreage in farms reached its maximum in New York State, but by 1950 less than half of the farmland remained (Thompson 1977). The area of forest in the eight counties in 1993 was between 27 and 65% (Alerich and Drake 1995).

Table 1 The percentage of each of the eight counties in the study that Census records show to have the condition of unimproved (U), improved (I), and total (T) farmland

Year	Allegany			Cattaraugus			Chautauqua			Erie			Genesee			Niagara			Orleans			Wyoming		
	U	I	T	U	I	T	U	I	T	U	I	T	U	I	T	U	I	T	U	I	T	U	I	T
1860	33	44	77	31	35	66	31	57	88	25	55	80	18	70	88	21	69	91	18	73	91	25	66	91
1870		54			43			63			64			74			75			76			75	
1880	28	64	92	27	50	77	23	75	97	17	75	92	15	84	99	11	80	92	13	88	101	20	89	109
1890	23	63	86	24	52	76	22	67	88	9	74	83	12	75	88	8	81	89	12	79	91	21	73	94
1900		62	90		50	80		64	90		64	85		77	93		84	91		82	95		71	97
1910																								
1920		50	86		41	77		53	87		59	81		69	87		79	87		79	92		61	92
1930			73			65			79			65			82			84			85			88
1940																								
1950			63			61			74			56			81			74			80			86

Years and variables with no data are shown as blank cells

Unimproved farmland land owned by a farmer that was typically either woodland, abandoned field, or swamp

Improved farmland either tilled, pasture, or orchard

Total farmland given in Census records for 1900 and later; calculated as sum of unimproved and improved land for earlier years

The PLSR and FIA data

The study area in western New York consisted of 162 townships surveyed by the HLC between 1797 and 1799. Most of the townships were of 9.6×9.6 km (1.6 km = 1 mile), but sizes of 6.4×9.6 and 9.6×11.2 km were also used (Fig. 1). Survey posts were erected at 0.8 km intervals along the township perimeter survey lines; the locations and species of two to four nearby trees of a post, known as bearing trees, were recorded, resulting in a total of 3,897 posts with 8,792 trees. Although estimated tree diameters were recorded in the public land surveys, we did not find such information in the private HLC township surveys used in this study. Also, unlike the public land surveys for which the finer section level data at 1.6×1.6 km were available (e.g., Brown 1998), the finer level data were not available for all the HLC townships and hence only bearing trees from the township perimeter surveys were used. As bearing trees were recorded at a fixed interval along the regular township survey lines, the HLC survey represented a relatively systematic sampling across the pre-settlement landscape for estimating pre-settlement forest conditions (Wang 2005).

The current forest conditions were derived from the most recent complete FIA survey of New York State, conducted between 1991 and 1993 (Forest

Inventory and Analysis Program (FIA Program 2008). Of the 764 plots recorded in the study area, 321 were naturally forested, each approximately 0.5 ha in size. Although the FIA survey structure is different from the relatively systematic HLC survey, no statistically significant broad-scale bias in the FIA plot locations was detected (Wang et al. 2009). Trees with diameter at breast height (dbh) ≥ 22.9 cm in the FIA survey were used for comparability with the HLC survey (Kronenfeld and Wang 2007), resulting in 4,303 trees dispersed among 261 plots.

Wang et al. (2009) suggested that the influence of the dissimilar HLC and FIA sampling schemes can be minimized by kriging at a coarse resolution, thereby providing spatially continuous estimation of broad-scale changes in forest distribution while ensuring that quantitative analyses are based on a sufficient number of samples from each survey. In order to minimize errors associated with small sample size and to increase confidence in spatial prediction, 17 predominant taxa were selected. Taxon composition was first computed at each HLC post from its corresponding bearing trees and at each FIA plot from its inventoried trees. Ordinary kriging was then performed separately for each taxon in ArcGIS (ESRI, Redlands, CA, USA) using the derived percent composition at the locations of the HLC posts and FIA plots to estimate the taxon's abundance

distribution in a grid of 9.6×9.6 km cells in the pre-settlement and present time periods (Wang et al. 2009). The selected grid-cell size corresponded to that of most of the HLC townships; a total of 162 grid cells were obtained.

The spatially resolved coverages of the 17 taxa's abundance distributions in the two time periods were obtained from Wang et al. (2009) and used as the input data in this study to calculate forest compositional turnover (FCT) and the three landscape metrics (see “Forest compositional turnover” and “Changes in taxon abundance and fragmentation of its distribution” sections below). In order to assess estimation uncertainty, we further calculated the root mean square error (RMSE) of point predictions of taxon abundances using the cross validation tool in ArcGIS. Cross validation removes a single point at a time from the point data set and predicts the value of that point using the kriging model. Following Isaaks and Srivastava (1989), a variance adjustment factor was calculated to scale the error estimates from point support to 9.6×9.6 km blocks. The adjusted RMSE averaged 3.1 and 4.5% for the HLC and FIA kriging estimates, respectively.

The 17 taxa accounted for 95.0 and 92.5% of the pre-settlement and current forests, respectively. Of these, three taxa were not used in the following analysis of life history characteristics because they were recorded in only one time period: American chestnut (*Castanea dentata*) declined precipitously due to disease and was not found in the FIA data; Scots pine (*Pinus sylvestris*) and apple (*Malus sylvestris*) were newly introduced into the study area. Of the remaining 14 taxa that existed in both time periods, 8 were decreaseers with a lower mean abundance in the FIA survey, and 6 were increaseers with the opposite.

Life history characteristics

In order to evaluate whether a taxon's changed abundance between the HLC and FIA surveys was related to successional status, this article compared changes in taxon abundances with seven life history characteristics commonly associated with early- and late-successional status (Huston and Smith 1987; Loehle 1988). Information on age at first reproduction, seed dispersal mechanism, maximum age, maximum height, seed weight, and shade tolerance

were obtained from Burns and Honkala (1990). Missing data on a taxon's maximum age and on maximum height were obtained from Farrar (1995) and on seed weight from Greenberg (2000). Information on heat content, a proxy for wood density and thus disease resistance (Loehle 1988), was obtained from Whitney (1996). These data were obtained for the 14 taxa that existed in both the HLC and FIA surveys. Since the data were not normally distributed, median values of each variable were employed for descriptive purposes, and non-parametric Spearman rank order correlation tests were used to relate the change in taxon abundance with the data on life history characteristics. Since seed dispersal mechanism is a categorical variable, however, Fishers exact test was used to test for significant differences just between the increaseer and decreaseer taxa.

Forest compositional turnover

The forest compositional turnover metric

The overall forest change for a given region k , such as a grid cell, was calculated as the FCT:

$$\text{FCT}_k = \frac{\sum_{i=1}^n |\text{FIA}_{ki} - \text{HLC}_{ki}|}{2}, \quad (1)$$

where n is the number of taxa, and FIA_{ki} and HLC_{ki} are, respectively, the current and pre-settlement percentage abundance of taxon i in the region k . The numerator sums the absolute differences between taxon abundances of the FIA and HLC surveys, while division by 2 results in complete turnover as percentage values. FCT is the inverse of the Sorenson similarity metric (McCune and Grace 2002) as applied to relative abundances. We calculate FCTs rather than use the Euclidean distance employed in some studies (e.g., Bürgi et al. 2000; Whitney and DeCant 2003), because we believe that FCT with its upper limit of 100% is more intuitive. The FCTs were calculated at three scales: for each of the 162 grid cells to compare with soil data; for each of the eight counties to investigate how forest clearance might have contributed to the observed change; and for the study area as a whole to compare with other studies in eastern North America. The county-scale FCT was calculated as the mean of the FCT values for all cells located in a county; cells that were partially present in two counties were weighted as being half in each county.

FCT and soil conditions

In order to evaluate whether the FCT was higher or lower in different soil conditions, FCT values for individual cells and for whole counties were compared with soil texture and soil drainage. There were a total of six texture and six drainage classes obtained from the State Soil Geographic (STATSGO) database of the USDA Natural Resources Conservation Service. Pearson's correlation coefficients (r) were calculated between the FCT and the percent of each cell or county that had a given soil texture or drainage class. Unlike some PLSR studies that measured vegetation-site relationships by overlaying tree data points directly with soil polygons (e.g., Dyer 2001), analyses here used FCT at the aggregated cell or county levels. It was not possible to measure FCT at a specific point, because HLC and FIA survey points were in different locations.

FCT and forest clearance at the county scale

The county-scale FCT was correlated with the county-scale indicators of forest clearance and forest retention. County-scale forest clearance was indicated using the mean percent of each county that was improved farmland and that was total farmland (improved plus unimproved), for the common period 1860–1890 (Table 1). County-scale forest retention was indicated as the mean percent of each county that was unimproved farmland for the common period 1860–1890 (Table 1). It was assumed that higher amounts of farmland would equate with higher forest clearance. As the grid cells in four of the counties come from only a portion of the county (Allegany 52%, Genesee 72%, Orleans 82%, and Wyoming 96%), while the farmland measures were an average for the whole county, we assume that the farmland measures were representative of the portion of the county for which we had data. County-scale forest recovery was indicated by the forest area in each county in 1993 from Alerich and Drake (1995).

Changes in taxon abundance and fragmentation of its distribution

Over the complete study area of 162 grid cells, the change in mean abundance of a taxon was related with three metrics of fragmentation of each taxon's

geographic distribution. The first was cell occupancy, calculated as the percentage of the 162 cells occupied by a taxon. Change in cell occupancy was calculated as percent occupancy in the FIA data minus that in the HLC data. Second, the number of patches within the distribution of each taxon was determined using FRAGSTATS (McGarigal et al. 2002). We used the 8-cell rule to define patches, meaning that a patch would consist of either one lone grid cell or a group of contiguous grid cells that shared either at least one edge or one corner. Change in patchiness was determined as the ratio of the number of patches in the FIA data divided by those in the HLC data. Third, FRAGSTATS was used to determine the contagion of each taxon's distribution. Contagion is defined as the probability of finding a grid cell containing a taxon adjacent to a cell that does not contain the taxon (Li and Reynolds 1993). Change in contagion was calculated as contagion in the FIA data minus contagion in the HLC data. Our calculation of these metrics is similar to those made by Delcourt and Delcourt (1996), except that we do so for individual taxon while they did so for vegetation communities. Pearson's correlation coefficients (r) were calculated between the changes in taxon's mean abundance and the three metrics with two different entrance levels, $>0\%$ and $\geq 1\%$, to assess the robustness of the relations. The entrance level of $> 0\%$ meant that values of a metric were calculated for all cells in which a taxon was present, whereas the entrance level of $\geq 1\%$ denoted that only cells with taxon abundances of at least 1% were used in calculations.

Forest age and understory composition

If changes in species composition were primarily related to successional status, then we would expect present forests to be trending toward the same species composition as found in the HLC data. In order to ascertain whether or not this is happening, the FIA plot data were grouped by stand age and dbh class, and taxon abundances for each group were compared with the HLC data. Plots assigned to one of six stand ages (5, 25, 45, 65, 85, and 105 years) by FIA surveyors were aggregated to three classes (5–25, 45–65, and 85–105 years) to ensure sufficient sample size within each class. An additional 49 plots for which stand age was recorded as –999 (indeterminate) were excluded from the analysis. Trees were assigned to one of three

dbh classes (0–22.8, 22.9–45.6, and ≥ 45.7 cm). Overall relative taxon abundances were computed by plot for each of the resulting nine combinations of stand age and dbh class; plot values were then averaged to determine overall relative abundances. Pearson's correlation coefficients (r) between the log-transformed abundances within each FIA age/dbh combination and the gridded HLC data were computed to test for significance. Under the assumption that pre-settlement forests were late-successional, it was hypothesized that correlations would be higher for older stands than for younger stands of a given dbh class and for smaller trees than for larger trees within a given age class.

Results

Life history characteristics of increasers and decreaseers

Changes of the taxon mean abundance were calculated using the grid-based estimates from kriging (cf. Wang et al. 2009). Of the 14 taxa found in both the HLC and FIA surveys, 6 were increasers and 8 were decreaseers (Table 2). Changed abundances of the 14 taxa found in both time periods were related to life history characteristics. The median values indicate that increasers, relative to decreaseers, tended to have: a younger age of first reproduction, a higher ratio of animal to wind seed dispersal, no difference in heat content (indicative of wood density), shorter maximum height, shorter maximum life, heavier seeds, and lower shade tolerance (Table 3). The tests indicated that maximum life, shade tolerance and, marginally, age at first reproduction were statistically significantly different, with maximum life remaining significant after Bonferroni adjustment.

Forest compositional turnover

General patterns in FCT

The FCT for the whole study area was 48.0% for the 17 analyzed taxa. When the FCT for the HLC data was calculated for each of the 162 cells using the 17 taxa with kriged records, the FCT ranged between 31.8 and 84.7%, with a mean of 57.0% (Fig. 2b). The

Table 2 Percent change of the taxon mean abundance based on kriging of the Holland Land Company (HLC) and Forest Inventory Analysis (FIA) data

Taxon	Scientific name	Change (%)
<i>Increasers</i>		
Ash	<i>Fraxinus</i> sp.	10.6
Red maple	<i>Acer rubrum</i>	9.1
Poplar, aspen	<i>Populus</i> sp.	9.1
Black cherry	<i>Prunus serotina</i>	8.9
Red oak	<i>Quercus rubra</i>	3.7
Hickory	<i>Carya</i> sp.	2.1
<i>Decreasers</i>		
Beech	<i>Fagus grandifolia</i>	–31.3
Sugar maple	<i>Acer saccharum</i>	–6.5
Hemlock	<i>Tsuga canadensis</i>	–3.3
Basswood	<i>Tilia americana</i>	–2.8
White oak	<i>Quercus alba</i>	–1.3
Yellow birch	<i>Betula alleghaniensis</i>	–1.2
Elm	<i>Ulmus</i> sp.	–1.0
White pine	<i>Pinus strobus</i>	–0.8

Increasers have a higher mean abundance in the FIA data set; decreaseers have the opposite

spatial pattern of FCT shows that counties located in the Erie-Ontario Lowland, such as Orleans and Genesee, have high levels of forest compositional change (Fig. 2c). Areas in the Appalachian Upland with high levels of change, such as in Cattaraugus county (Fig. 2b, c), appear to occur in cells where the two introduced species (Scots pine and apple) exhibit major increases (cf. Wang et al. 2009, p. 84).

Soil conditions and FCT

At the grid-cell scale ($n = 162$), FCT was significantly positively correlated with the percent of a cell that was very-fine sandy loam ($r = 0.32$, $P < 0.001$) and was significantly negatively correlated with the percent of a cell that had a drainage of somewhat excessive ($r = -0.23$, $P = 0.004$). However, those classes only cover, respectively, 2.1 and 0.2% of the study area. At the county scale ($n = 8$), FCT was both significantly positively correlated with the percent of a county that was muck ($r = 0.73$, $P = 0.048$) and that was very poorly drained ($r = 0.87$, $P = 0.006$). However, these two classes only cover, respectively, 1.4 and 0.8% of the study area. Significant

Table 3 Median values of life history characteristics of taxa that decrease and taxa that increase in abundance from the pre-settlement HLC to the current FIA surveys

Life history characteristic	Decreasers ($n = 8$)	Increases ($n = 6$)	r_s	P
Age of first reproduction (years)	17.5	15.0	-0.438	0.058
Dispersal ($a =$ animal, $w =$ wind)	$3a/5w$	$3a/3w$	na	0.373
Heat content (kJ/m^3)	5.6	5.6	-0.210	0.237
Maximum height (m)	30.8	26.5	-0.272	0.173
Maximum life (years)	275	150	-0.658	0.005
Seed weight (g)	0.041	0.060	-0.114	0.348
Shade tolerance (3 = tolerant, 2 = intermediate, 1 = intolerant)	2.5	2.0	-0.554	0.020

P values are from Fishers exact test for differences in increasers and decreasees for the categorical variable of dispersal, and from Spearman rank order correlations with change in mean percent abundance in the FIA and HLC data for the other variables

correlations were not obtained between FCT and any other soil texture or drainage classes.

FCT and forest clearance at the county scale

At the county scale ($n = 8$), for the common interval of 1860–1890, FCT was significantly positively correlated with the mean area of improved farmland ($r = 0.75$, $P = 0.016$) and positively but non-significantly correlated with the total area of farmland ($r = 0.57$, $P = 0.070$). The correlation between FCT and the mean area of improved farmland between 1860 and 1920 was unchanged and between FCT and mean area of total farmland between 1860 and 1950 was higher ($r = 0.70$, $P = 0.026$). The FCT was negatively correlated with the mean area of unimproved farmland between 1860 and 1890 (excluding 1870) ($r = -0.58$, $P = 0.068$) and significantly negatively correlated with the total area of forest in each county in 1993 ($r = -0.66$, $P = 0.037$). A multiple-regression between FCT (dependent variable) and mean areas in improved and unimproved farmland (independent variables) yielded regression parameters that were not statistically significant but positive for improved farmland and negative for unimproved farmland ($R_{\text{adj}}^2 = 0.39$, $p = 0.125$).

Changes in taxon abundance and fragmentation of its distribution

At the scale of the complete study area, as the change in a taxon's mean abundance increased so too did the change in the percent of the cells that the taxon occupied (Fig. 3a). The strength of this relationship ($n = 14$ taxa) remained constant when the entrance

level changed from 0% ($r = 0.60$, $P = 0.024$) to 1% ($r = 0.60$, $P = 0.023$). An extreme case is beech that changed the most in mean abundance (-31.3%), but did not decrease much in cell occupancy (Fig. 3a). When beech was excluded from the analysis, the strength of the relationship ($n = 13$) increased for entrance levels at both 0% ($r = 0.69$, $P = 0.01$) and 1% ($r = 0.79$, $P = 0.001$).

Change in the patchiness of a taxon's distribution, generally increased for taxa whose mean abundance decreased, and decreased for taxa whose mean abundance increased (Fig. 3b). Values of patchiness above one indicate an increase in the number of patches, while values below one indicate a decrease. The correlations remained negative as the entrance level changed from 0% ($r = -0.85$, $P < 0.001$) to 1% ($r = -0.84$, $P < 0.001$). When beech was excluded, the strength of the correlation decreased for both the entrance levels 0% ($r = -0.64$, $P = 0.017$) and 1% ($r = -0.53$, $P = 0.062$).

Contagion of a taxon's distribution generally decreased for taxa whose mean abundance decreased and increased for taxa whose mean abundance increased (Fig. 3c). The correlations remained positive when the entrance level changed from 0% ($r = 0.70$, $P = 0.005$) to 1% ($r = 0.67$, $P = 0.008$) and increased for both the entrance levels 0% ($r = 0.76$, $P = 0.003$) and 1% ($r = 0.70$, $P = 0.007$) when excluding beech.

Changes in fragmentation at different entrance levels can be seen for beech, the greatest decreasee, and red maple, the second greatest increaser (Fig. 4). Between the 1790s and 1990s, beech's cell occupancy decreased, patchiness increased, and contagion decreased, while red maple's distribution did the opposite.

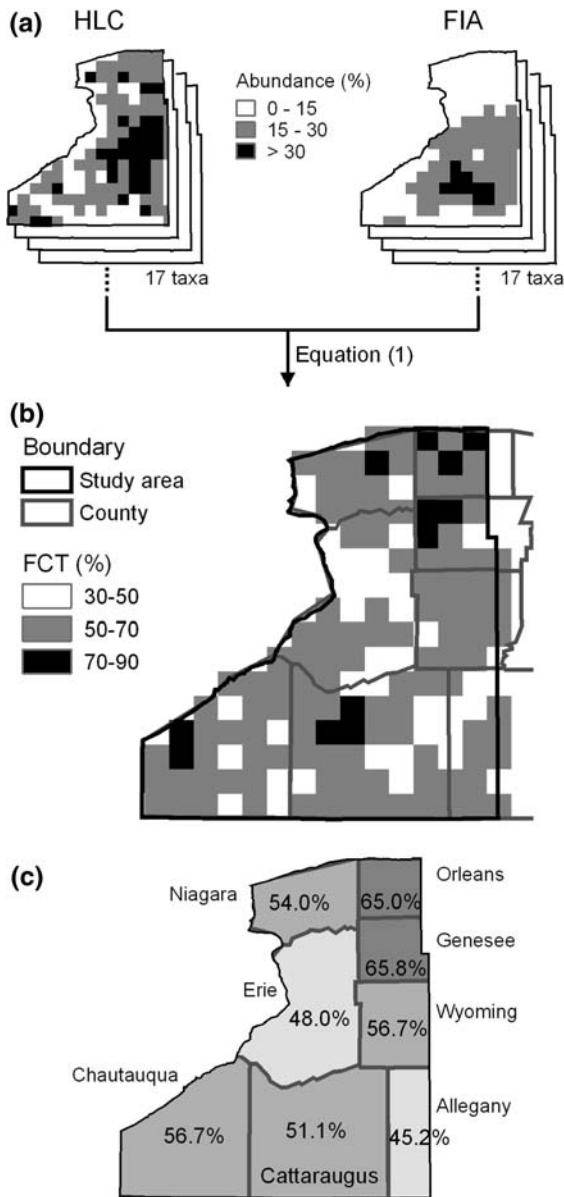


Fig. 2 Schematic diagram illustrating the derivation of forest compositional turnover (FCT) at different scales. **(a)** The patterns in the top layer are sugar maple. **(b)** FCT of the 162.9.6 × 9.6 km grid cells. **(c)** County-scale FCT calculated as the mean of the FCT values using all cells located in a county from **(b)**

Forest age and understory composition

Log-transformed overall abundances of the 14 taxa in the HLC and plot-level FIA data sets were uncorrelated ($r = 0.01, P = 0.48$; results not shown). When FIA data were grouped by dbh and stand age,

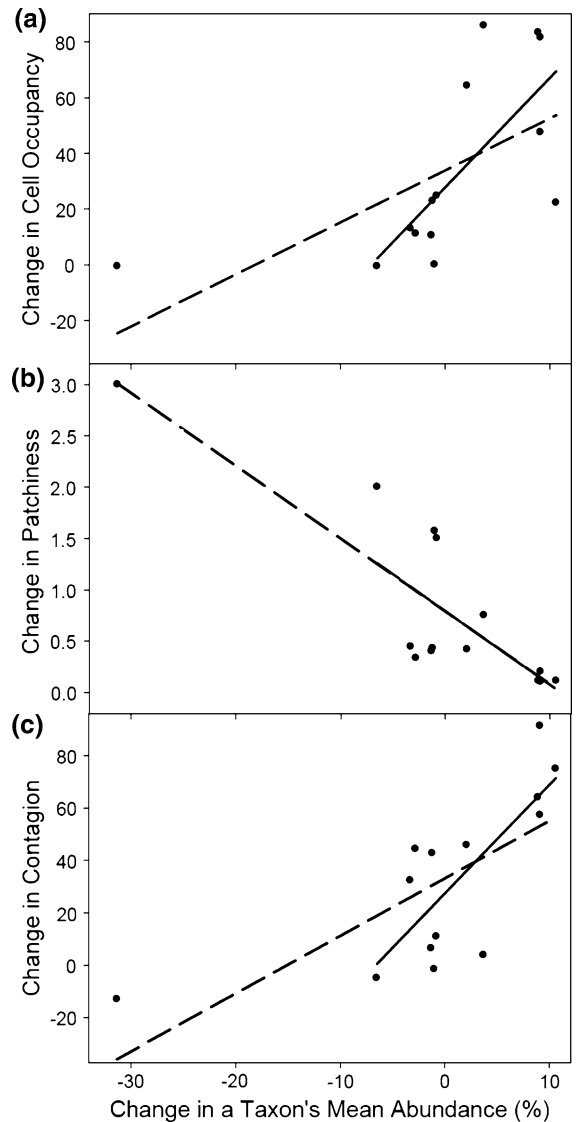


Fig. 3 Relations between change in mean abundance of a taxon between FIA and HLC data and change in a taxon's **(a)** cell occupancy at the entrance level of >0% **(b)** patchiness **(c)** contagion. Analyses exclude taxa that existed in only one time period. *Dashed* and *solid* lines are linear trend lines with and without beech, respectively

however, significant relationships emerged between the HLC and three of the nine FIA groupings (Fig. 5). Abundances of taxa among small trees (<22.9 cm dbh) in young (5–25 years) FIA stands (Fig. 5a) showed no correlation with the HLC data ($r = -0.06, P = 0.71$). As stand age increased, however, so did the strength of the correlation with the HLC, with taxon abundances for small trees in

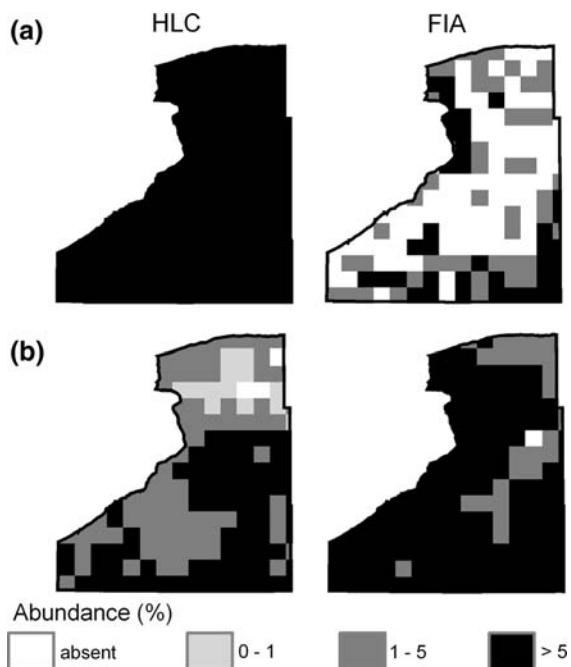


Fig. 4 Spatial patterns of change in the 9.6×9.6 km grid cells for (a) the most marked decrease, beech, and (b) the second greatest increase, red maple

middle-aged (45–65 years) FIA stands (Fig. 5b) showing moderate correlation ($r = 0.29$, $P = 0.02$) and for small trees in older (85–105 years) FIA stands (Fig. 5c) showing strong correlation ($r = 0.69$, $P = 0.0001$). The only other FIA data group that showed marginally significant correlation with the HLC data was that of large (≥ 45.7 cm) trees in the youngest (5–25 years) stands ($r = 0.18$,

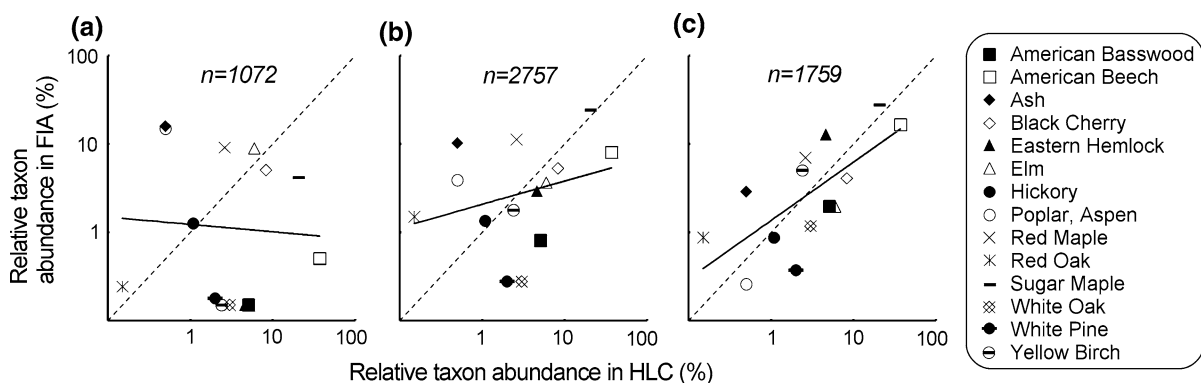


Fig. 5 Relative taxon abundances in the HLC data versus three subsets of the FIA data of the smallest trees (<22.9 cm dbh) by stand age: (a) 5–25, (b) 45–65, and (c) 85–105 years. Sample size (n) indicates number of trees in FIA

$P = 0.06$; results not shown). Closer examination revealed that this group consisted primarily of relict trees that were much larger than others in the same plot.

Discussion

Life history characteristics of increasers and decreaseers

The general pattern of forest change in western New York was a decline in late-successional taxa and an increase in early-successional taxa (Fig. 4). This pattern, noted by others (Abrams and McCay 1996; Dyer 2001), is most strongly related to the life history characteristics of maximum life and secondarily to shade tolerance (Table 3). Although Montoya et al. (2008) suggested that animal dispersal of seeds was important in fragmented landscapes, we did not find a significant relationship between dispersal mechanism and changed abundance of a taxon. The results for the other life history characteristics were not statistically significant, but the differences in median values of increasers, relative to decreaseers, conformed to what has been suggested by other studies (Huston and Smith 1987; Loehle 1988) to be traits of early-successional taxa, such as a younger age of first reproduction and a shorter maximum height. That only three of the seven characteristics exhibited significant differences may result from characteristics needing to be fit into more complex functional groups

data subset. Fourteen taxa whose life history characteristics were obtained were analyzed. *Solid lines* are the best-fit lines for the regression. *Dashed lines* show the 1:1 lines

that take into account environmental variables, such as soil conditions (e.g., Hérault and Honnay 2007), in addition to FCT. Although only maximum life remains significant after Bonferroni correction, all relationships were in the expected direction, a result unlikely to occur due to chance.

Forest compositional turnover

The FCT for the whole study area of western New York was 48.0%. This value was similar to the mean FCT of 44.9% (range: 22.1–67.8%) that we obtained using published records for 26 other sites (and subdivisions of sites, if given) in the northeastern and Midwestern USA (Whitney 1996, pp. 159, 196, 204; Bürgi et al. 2000; Dyer 2001; Whitney and DeCant 2003; Friedman and Reich 2005). This suggests that forests through much of the northeastern and Midwestern USA are almost half changed from their pre-settlement composition.

FCT and soil conditions

Although prior research on land-cover change since the pre-settlement suggested that soil was one of the important factors controlling agricultural conversion (Rhemtulla et al. 2007), we only found significant correlations between FCT and soil conditions for <5% of the study area that was muck and very poorly drained. Our calculation of FCT using percent composition of pre-settlement and present tree taxa in published records (i.e., Whitney and DeCant 2003, p. 1692; Friedman and Reich 2005, p. 734) suggested similar results; we were not able to determine the correlation between FCT and soil conditions in those studies, however, because information on the percent of study area in each soil type was not provided. The calculation of the data in Friedman and Reich (2005) showed that the FCTs by soil texture ranged from 25.1 to 40.3%; a FCT of 40.0% in organic soil in their study did agree with our finding that organic soils had higher FCTs. On the other hand, the four county area of northwestern Pennsylvania in Whitney and DeCant (2003) had similar FCTs in their beech–sugar maple forest type on soils of finer textured and imperfectly drained (FCT = 51.7%) and their white oak–chestnut forest type on soils derived from weathered sandstone, representing drier habitats (FCT = 55.2%).

The minimal relations between FCT and soil in the HLC study area are surprising given that HLC surveyors noted that fine textured soils were higher quality agricultural land (Wyckoff 1988) and a higher FCT would then be expected. Indeed, based on soil quality and topography, the southern-most cells in Cattaraugus County appeared to have the lowest agricultural quality, but exhibit a FCT in the range of 50–70% (Fig. 2b). Since that area was low quality for agriculture, the high FCT suggested that the land might have been logged. However, logging would not just occur on low quality soils, but on all soil conditions, thereby over-riding the agriculture-related pattern.

We have not been able to find sub-county scale spatially resolved historical records on the type of agriculture or logging that would allow us to relate specific forms of human disturbance with specific changes in tree taxon abundance. It is possible that a comparison of finely resolved PLSR line descriptions of soil and vegetation with a modern re-survey of the existing vegetation and soil would find stronger relations between soil conditions and FCT. Indeed, a study in adjacent central New York that employed a 50 × 50 m grid found that agricultural lands that were abandoned to natural reforestation were more common in areas with steeper slopes, a greater distance to roads, and lower soil lime content (Flinn et al. 2005).

FCT and forest clearance at the county scale

Forest compositional turnover was highest in counties that had the greatest amount of forest cleared for improved farmland and the least area remaining as unimproved woodlot left in the farmland (Table 1; Fig. 2c). The clearance of large areas of farmland likely subdivided the old growth forest of late-successional species into smaller and more isolated patches. Those small patches probably experienced an enhanced edge effect which would favor shade-intolerant early-successional species over shade-tolerant late-successional species (Table 3; Kupfer et al. 2006). Selective logging of relic woodlots may also have occurred for late-successional species with high heat contents (Whitney 1996) and of hemlock for chemical wood industries such as tanning (Russell et al. 1993). The effect of unimproved farmland, likely in the form of woodlots on

each farmer's field, may be similar to the seed source effect provided by the retention trees and patches employed in modern ecological forestry (Lindenmayer and Fischer 2006).

Changes in taxon abundance and fragmentation of its distribution

The abandonment of large areas of farmland would have resulted in initial colonization primarily by early-successional species, which would have also been abundant in the relictual woodlots that experienced selective logging and an enhanced edge effect. The regrowth of the abandoned farmlands with early-successional species that were previously restricted primarily to natural disturbance gaps, which were typically quite small in the northeastern USA (Runkle 2000), allowed their geographic distributions to agglomerate increase in contagion and decrease in patchiness (Figs. 3, 4).

Although necessary to produce grids of predicted taxon abundance used for calculating the landscape metrics of contagion and patchiness, the kriging process and resultant coarse resolution would have some smoothing effects on the FCT values. Wang et al. (2009) examined how differences in the density of sampling locations of the HLC and FIA data sets might have influenced the spatial structure of the estimated taxon distribution patterns and suggested that the general trend of forest change remained similar. Although the degree of smoothing would be affected by the sampling scheme, because our analyses compared one taxon with another, any such effects would apply equally to every taxon. Differences in the change of landscape metrics of patchiness and contagion between taxa should thus be a result of differences in the change of individual taxon distributions, rather than the kriging process. We could not conduct a multi-resolution analysis to investigate the effects of resolution, because the data do not allow it. However, prior PLSR studies have suggested similar resolutions to ours for presenting pre-settlement vegetation patterns of a large area of several counties (Friedman and Reich 2005; Wang and Larsen 2006). That the relations between a taxon's mean abundance and these landscape metrics were robust to different entrance levels suggests that resolution does not unduly influence the ecological interpretation.

Forest age and understory composition

As large patches of early-successional forest age, it is interesting to consider if modern forests will become similar in species composition to pre-settlement forests. The composition of small trees (<22.9 cm dbh) in the oldest (85–105 years) FIA plots shows remarkable similarity to the HLC data (Fig. 5c), and if these represent future dominants then the possibility exists that forests will return to something akin to their prior state. These results are similar to the widespread “mesophication” of the oak- and pine-dominated forests of the eastern USA that has followed fire suppression (Nowacki and Abrams 2008), as in both cases shade-tolerant species have increased in abundance while shade-intolerant species adapted to disturbance have decreased in abundance.

The results indicate that the primary goal of restoration would be to increase the abundance of beech (Fig. 4). Beech does appear to be increasing in abundance in the <22.9 cm dbh fraction of the forest, but only in forests older than ~100 years (Fig. 5c). In fact, beech recruitment in the understory is abundant enough in New York State that foresters are developing logging methods that will limit beech recruitment and its impending forest dominance at the expense of more commercially viable species (Bohn and Nyland 2003). This may indicate that, as suggested in Fig. 5, successional time may be adequate to enable the return of beech to its pre-settlement dominance. Also, according to Wang et al. (2009), the spatial patterns of change for sugar maple, hemlock, and white oak have revealed local declines that are as large as those of beech, and are thus deserving of restoration in those locations.

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