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AGRICULTURAL LEGACIES IN FOREST ENVIRONMENTS: TREE COMMUNITIES, SOIL PROPERTIES, AND LIGHT AVAILABILITY

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Abstract. Temperate deciduous forests across much of Europe and eastern North America reflect legacies of past land use, particularly in the diversity and composition of plant communities. Intense disturbances, such as clearing forests for agriculture, may cause persistent environmental changes that continue to shape vegetation patterns as landscapes recover. We assessed the long-term consequences of agriculture for environmental conditions in central New York forests, including tree community structure and composition, soil physical and chemical properties, and light availability. To isolate the effects of agriculture, we compared 20 adjacent pairs of forests that were never cleared for agriculture (primary forests) and forests that established 85–100 years ago on plowed fields (secondary forests).

Tree communities in primary and secondary forests had similar stem density, though secondary forests had 14% greater basal area. Species composition differed dramatically between the two forest types, with primary forests dominated by *Acer saccharum* and *Fagus grandifolia* and secondary forests by *Acer rubrum* and *Pinus strobus*. Primary and secondary forests showed no consistent differences in soil physical properties or in the principal gradient of soil fertility associated with soil pH. Within stands, however, soil water content and pH were more variable in primary forests. Secondary forest soils had 15% less organic matter, 16% less total carbon, and 29% less extractable phosphorus in the top 10 cm than adjacent primary stands, though the ranges of the forest types mostly overlapped. Understory light availability in primary and secondary forests was similar.

These results suggest that, within 100 years, post-agricultural stands have recovered conditions comparable to less disturbed forests in many attributes, including tree size and number, soil physical properties, soil chemical properties associated with pH, and understory light availability. The principal legacies of agriculture that remain in these forests are the reduced levels of soil organic matter, carbon, and phosphorus; the spatial homogenization of soil properties; and the altered species composition of the vegetation.

Key words: agriculture; disturbance; forest; land-use history; light; old-field succession; ordination; restoration; soil; tree.

INTRODUCTION

Human land use has transformed temperate deciduous forests worldwide. Throughout Europe and eastern North America, converting forests to agricultural fields destroyed and fragmented extensive areas of continuous habitat, while later farmland abandonment created new forests on cleared lands (Rackham 1986, Williams 1989). Forests growing on former agricultural fields comprise over half of current forest cover in many regions (Vellend 2003). Though these widespread, common habitats hold great potential for the restoration of biological diversity in reforested landscapes, it is unclear how much post-agricultural forests will grow to resemble the communities they replaced and how long full recovery may take. Even centuries after abandonment, plant community composition, structure, and function in these forests often remain distinct from forests never cleared for agriculture (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1996, Koerner et al. 1997). In particular, post-agricultural forests consistently lack the diversity of herbaceous species characteristic of less disturbed temperate deciduous forests (Peterken and Game 1984, Dzwonko and Loster 1989, Matlack 1994, Bossuyt et al. 1999, Singleton et al. 2001, Vellend 2004). Since herbs comprise the majority of plant species richness in temperate forests, their recovery is a primary concern.

Facilitating recolonization by native plants in landscapes recovering from agriculture requires an understanding of the processes that control species distributions across habitats of different history. Since successful colonization involves both the ability to disperse to new sites and the ability to establish and persist in new habitats, a key goal is to evaluate the relative roles of dispersal ability vs. environmental interactions. Most studies of post-agricultural colonization have focused on dispersal, which appears to limit the distributions of many herbaceous species (Ehrlén

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and Eriksson 2000; reviewed by Flinn and Vellend 2005). However, environmental conditions in post-agricultural forests may also differ, and much less is known about how habitat quality contributes to the colonization process.

A necessary first step is to assess the effects of historical agriculture on current forest environments. Soil changes following cultivation and during early stages of forest regrowth have received the most thorough study. In temperate regions, cultivation reduces soil carbon by an average of 30% (Post and Mann 1990, Johnson 1992, Davidson and Ackerman 1993, Murty et al. 2002). As forests develop on old fields, numerous studies have found that soil acidity increases and organic matter, carbon, and nitrogen reaccumulate (Billings 1938, Thorne and Hamburg 1985, Richter et al. 1994, Hooker and Compton 2003). The immediate consequences of clearing and abandoning farmland are thus well documented, but the magnitude and persistence of these changes have been surprisingly variable among regions. In northern France, for example, soil texture and chemistry remained altered from Roman agriculture 2000 years before (Dupouey et al. 2002), and other sites showed agricultural legacies in forest soils for at least a century (Koerner et al. 1997, Wilson et al. 1997, Verheyen et al. 1999, Compton and Boone 2000). By contrast, some former agricultural fields have largely recovered the soil characteristics of forests never cleared for agriculture within 100 years (Kalisz 1986, Compton et al. 1998, Dzwonko 2001, Graae et al. 2003). The strength of lasting effects depends on complex interactions between initial site conditions and the nature, duration, and intensity of agricultural use. Studies focused solely on soil properties have thus found unpredictable results, while few have attempted to characterize other aspects of the environment such as light or moisture regimes (Dzwonko 2001, De Keersmaeker et al. 2004).

Also often ignored are agricultural legacies in the spatial heterogeneity of environmental conditions. Besides altering mean levels of resource availability, cultivation likely changes the degree and spatial scale of variability. For example, much forest-floor heterogeneity is created when trees uproot to form pits and mounds; the resulting gradients in soil acidity, temperature, moisture, litter cover, and humus depth influence small-scale species distributions (Beatty 1984). Plowing levels this microtopography, which is not regained until mature trees begin to fall. Several studies suggest that spatial homogenization may persist in post-agricultural forests for at least 100 years (Wilson et al. 1997, De Keersmaeker et al. 2004, Fraterrigo et al. 2005). If small-scale variation in soil properties contributes to the maintenance of diversity in forest plant communities, then the homogenization caused by agriculture could hinder the recovery of species richness in post-agricultural forests.

Another important limitation on efforts to assess agricultural impacts is the relationship between land-use patterns and preexisting environmental variation. Since physical factors such as slope and drainage influence which lands people clear and abandon, land use and prior conditions are often confounded (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1996, Matlack 1997). In many landscapes, these associations make it difficult to distinguish the effects of land use from inherent site differences. Clearly, the full and long-term consequences of agriculture in forested landscapes remain incompletely understood, and building such knowledge becomes increasingly important as deforestation for agriculture continues in many parts of the world.

Here we investigate the legacy of agriculture in central New York forests by comparing environmental conditions between forests that developed on plowed fields 85–100 years ago (secondary forests) and forests that were never cleared for agriculture (primary forests; sensu Rackham 1980, Peterken 1981). Our primary goal is to characterize the abiotic environments experienced by herbs and tree seedlings in the two forest types. Thus, we cover the principal environmental gradients relevant to understory plants (soil nutrients, water, and light availability), and we quantify within-stand variation in these resources. Since the tree canopy mediates all aspects of the environment in the forest understory, we also characterize tree community structure and composition in the two forest types. Previous work emphasized the need to control for initial conditions, as topography and soils strongly influenced the geographical distribution of land uses in this landscape (Flinn et al. 2005). To isolate the effects of agricultural history, we used a paired design where adjacent primary and secondary forests share similar topography and soil types. Past results from central New York also suggested that differences between primary and secondary forest soils may be subtle compared to natural variation across the landscape (Flinn et al. 2005). Thus, we designed a more comprehensive study of tree communities, soil physical and chemical properties, and light availability, replicated across a heterogeneous landscape representative of much of the northeastern United States.

Study Area

Climate, topography, soils, and vegetation

We conducted this study throughout Tompkins County, which occupies 1250 km^2 in central New York state (42°26′ N, 76°30′ W), USA. The region has a humid, continental climate with a mean annual temperature of 8°C and a mean annual precipitation of 90 cm (Northeast Regional Climate Center 2005). The land lies on the rolling Allegheny Plateau, with elevations ranging from 120 to 640 m above sea level. The Devonian bedrock and overlying glacial till predominantly consist of shale, siltstone, and sandstone but also contain some limestone. Soils include loamy, mixed, mesic Alfisols and

Inceptisols that range in pH from about 4 to 7 (Neeley 1965). Most are moderately fertile silt loams. The vegetation falls into the Allegheny section of Braun's (1950) hemlock–white pine–northern hardwoods region. Mesic, upland forests dominated by *Acer saccharum* and *Fagus grandifolia* cover much of the landscape (Marks and Gardescu 1992, Mohler et al. 2006).

Land-use history

Tompkins County was almost completely forested prior to European settlement in 1790 (Marks and Gardescu 1992). Clearing for agriculture accelerated after 1850, reducing forest cover to 19% of the land area in 1900, at the height of agricultural activity (Smith et al. 1993). Dairy farming was the predominant form of agriculture. In 1930, for example, 21% of the county's land area was devoted to pasture, 21% to hay, 18% to other crops, 34% to woods, brush, and fallow, and 6% to other uses such as villages, houses, and roads (Lewis 1934). Widespread farm abandonment in the early 1900s allowed forests to reclaim much of the landscape, and by 1995 forests covered 54% of the county (Flinn et al. 2005).

Methods

Sites

During the 2004 growing season, we characterized environmental conditions in 20 pairs of adjacent primary and secondary forests. We chose mesic, upland sites where the two stands had a similar slope, aspect, elevation, and soil type (Singleton et al. 2001; Appendix). Many of the land-use boundaries coincided with property lines, further suggesting that ownership patterns rather than environmental discontinuities determined differences in land-use history within these sites. Aerial photographs from 1936 to 1938 and subsequent years allowed us to distinguish primary from secondary forests and to select secondary forests 85–100 years old (Smith et al. 1993).

We follow Rackham (1980) and Peterken (1981) in defining primary forests as sites that have remained continuously wooded throughout the historical period, while secondary forests originated on former agricultural land. Most primary forests are not old-growth. Though never cleared for agriculture, virtually all primary forests in the central New York landscape have been selectively cut, and some were grazed by livestock, primarily cattle. However, the primary forests we studied were neither logged nor grazed so heavily that they lacked a closed tree canopy in 1936–1938 and subsequent aerial photographs. We also avoided stands that showed evidence of logging within the past 20 years. These primary forests therefore represent the least-disturbed forests that allow for the paired, replicated comparisons we conduct here. The crucial difference between the forest types in this study is that the primary forests, while disturbed to some extent, remained as forests, whereas the secondary forests were fully cleared, plowed, and converted to agricultural fields.

All of the secondary forests we selected had once been plowed. We identified previously plowed areas by the complete absence of treefall pits and mounds, which could only have been caused by cultivation. In central New York, plow layer (Ap horizon) boundaries can be indistinct, whereas the lack of microtopography is a simple and reliable indicator of historical plowing. Upland forests in this region have distinctive pit-and-mound topography, so the sharp, linear transition to a smooth forest floor made adjacent plowed sites readily distinguishable (see Plate 1). The presence of stone piles or walls, which are relatively uncommon in central New York and occur only where stones have been removed from plowed fields, often corroborated this interpretation (Marks and Gardescu 2001). It is likely that some or all of the secondary forests were also used as pastures at some time in their history. Farmers often cropped and pastured lands in rotation, and it was common to pasture animals in fields taken out of cultivation before abandoning them completely (Vaughan 1928). However, we excluded sites that had been only pastured and not plowed.

While it is impossible to know which crops were grown on specific fields, county agricultural census records from 1855 to 1925 show that hay (often *Phleum pratense*), oats (*Avena sativa*), buckwheat (*Fagopyrum esculentum*), and corn (*Zea mays*) covered the greatest acreages (Walrath 1927). The fields we studied were abandoned by 1920, before the widespread use of inorganic fertilizers, but they may have received manure, lime, or other amendments. Manure applications were probably relatively light, since livestock densities were quite low compared to other landscapes in New England and Europe (e.g., Compton and Boone 2000). During the 1800s and early 1900s, farms in Tompkins County covered an average of 100 acres (0.4 km^2) and had an average of 6–10 cattle (Walrath 1927). The tenure of cultivation may have been relatively brief. Secondary forests in this study probably spent fewer than 50 years in agriculture, as the majority of forest clearing took place after 1850, and widespread abandonment began shortly after 1900. Many of the sites have less favorable topography and soils for farming than nearby areas (Neeley 1965; Appendix), so they may have been among the last to be cleared as well as the first to be abandoned (Flinn and Marks 2004, Flinn et al. 2005).

Each stand covered at least one hectare, and we conducted all sampling along four transects perpendicular to the land-use boundary, 100 m long and 20 m apart.

Tree communities

To describe the tree communities, we recorded the species and diameter at breast height (dbh) of all stems $\geq$10 cm dbh in 100 m^2 circular plots. We sampled 10 plots per stand, at random positions along the four transects, so that the area sampled in each stand summed to 0.1 ha. These data yielded the stem density (stems/ha), basal area (m^2/ha), and relative basal area (percentage of total basal area in each stand) of each species.

Soil physical properties

We measured bulk density by the excavation method (Grossman and Reinsch 2002), which is most appropriate for rocky forest soils (Page-Dumroese et al. 1999). Between 14 June and 8 July, four small excavations were made in each stand, one on each transect at a random position. After removing intact leaf litter (the Oi horizon), we dug a pit 15 × 15 cm wide and 10 cm deep using a wooden frame, a ruler, and a machete. We dried the excavated soil in ovens at 60°C and weighed it, then sieved the soil and measured the mass and volume of rocks to determine the concentration of coarse fragments (mineral particles $>$ 2 mm) and the bulk density of the fine-earth fraction.

At the same locations where we sampled bulk density, we also described the organic horizons comprising the forest floor. To quantify the amount of leaf litter (Oi), we collected all litter within a 0.1-m^2 frame, oven-dried it, and weighed it. We measured the depth of the humus layer (Oe and Oa) on the four faces of the excavated pits. Since exotic earthworms have a major impact on both litter quantity and humus depth (Bohlen et al. 2004, Suárez et al. 2006), we also noted the presence or absence of earthworm activity, which was visually evident in casts, burrows, and midden piles. Earthworm activity at each site was quantified as the number of pits with worms.

Soil chemical properties

Soil samples were collected by removing intact leaf litter (Oi), then taking cores 2 cm in diameter and 10 cm deep. This depth was chosen because the top 10 cm contain most roots of herbaceous plants and tree seedlings. We collected 20 cores from each stand, evenly spaced along the four transects, from 14 June to 8 July.

To determine water content, soil cores were weighed immediately, air-dried for at least one week, and weighed again. Soil water contents fluctuate with weather conditions, making them difficult to compare across sites sampled at different times. However, since paired stands were sampled on the same day or on consecutive days, within-pair comparisons are valid. We used the soil moisture measurements only to compare the relative soil moisture status of adjacent, paired stands, not the absolute soil moisture levels of different sites.

To gain a measure of intra-site variability, we calculated coefficients of variation among the 20 individual samples from each stand for both water content and pH. After weighing, we ground each soil core through a Wiley mill with 0.85-mm mesh and measured its pH in a 1:2 soil : water suspension. The cores were then combined into a composite for further analysis.

Total carbon (C) and nitrogen (N) were determined by elemental analyzer (FlashEA 1112, CE Elantech, Lakewood, New Jersey, USA) using 7 mg of soil. We used the mean of two analyses from each sample. Organic matter content (OM) was measured by loss on ignition at 500°C for 2 h. Though loss on ignition may overestimate organic matter content due to losses of carbonates and structural water from clay minerals, carbonates do not decompose below 750°C (Nelson and Sommers 1996), and loam soils lose minimal amounts of structural water ($<$4%; Ball 1964), so this method yielded accurate estimates of organic matter content for these soils.

The Cornell Nutrient Analysis Laboratories (Cornell University, Ithaca, New York, USA) analyzed soil samples for extractable nutrient concentrations including phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), aluminum (Al), iron (Fe), copper (Cu), manganese (Mn), and zinc (Zn). Nutrients were extracted with Morgan's solution (10% sodium acetate in 3% acetic acid, buffered to pH 4.8; Morgan 1941). Nutrient concentrations were determined by atomic absorption spectrophotometry, except phosphate, which was measured colorimetrically by stannous chloride reduction.

Soil nutrient concentrations were measured on the basis of mass, as the mass of each nutrient per kilogram of dry soil (mg/kg). But nutrient concentrations per volume may have more biological significance, since they represent the amount of nutrients available to root surfaces (Federer et al. 1993). Therefore we used the bulk density measurements to convert gravimetric nutrient concentrations to a volume basis, and we report the mass of each nutrient in the volume of soil in the top 10 cm of one hectare (kg/ha).

Light availability

We quantified understory light availability using hemispherical photographs of the forest canopy. This method gives a precise characterization of canopy structure and allows for estimation of light availability throughout the year (Rhoads et al. 2004). Between 12 August and 8 September, we took 20 photographs in each stand, spaced evenly along the four transects. Photographs were taken on overcast days or at dawn or dusk to avoid glare from direct sunlight. For each photograph, the camera was positioned at 0.75 m above the ground, aligned with north, and leveled horizontally. We used a Nikon Coolpix 5700 digital camera with a Nikon FC-E9 Fisheye Converter (0.2 times magnification, 180° view angle, 7-mm combined focal length; Nikon, Tokyo, Japan).

We analyzed the digital images with the Gap Light Analyzer program (Frazer et al. 1999). We specified the growing season as 15 May to 30 September, and the Appendix provides other site attributes the program

TABLE 1. Tree community structure and species composition of primary and secondary forests in central New York.

	Density (stems/ha)		Basal area (m^2/ha)		Relative basal area (%)			
Tree species	Primary	Secondary	Primary	Secondary	Primary	Secondary	*t*	*P*
Acer rubrum	80	202	4.3	12.7	14	37	−3.98	0.0008
Acer saccharum	142	88	8	2.6	26	7.6	3.99	0.0008
Amelanchier arborea	0	5	0	0.2	0	0.5	−1.9	0.0722
Betula lenta	9	22	0.2	0.8	0.7	2.4	−1.72	0.1012
Betula lutea	3	1	0.1	0	0.2	0	1.72	0.1013
Carya cordiformis	2	23	0.1	1.2	0.3	3.5	−1.19	0.2486
Carya ovata	5	3	0.2	0.3	0.6	0.8	−0.57	0.5722
Fagus grandifolia	112	7	5.2	0.1	17	0.3	4.09	0.0006
Fraxinus americana	39	86	2.4	3.9	7.9	11	−1.35	0.1942
Ostrya virginiana	18	26	0.3	0.3	1	1	−0.45	0.6598
Pinus strobus	1	56	0.1	6	0.3	17	−4.44	0.0003
Populus grandidentata	8	6	0.5	0.7	1.8	1.9	−0.35	0.7332
Populus tremuloides	7	15	0.5	1.2	1.6	3.4	−1.71	0.1043
Prunus serotina	5	13	0.5	1.5	1.7	4.2	−0.83	0.4156
Quercus alba	0	2	0	0.1	0	0.2	−1.23	0.2321
Quercus rubra	22	22	3	1.7	10	4.9	1.73	0.0999
Tilia americana	22	4	1.7	0.4	5.6	1	2.32	0.0319
Tsuga canadensis	87	9	3.2	0.3	11	0.8	3.15	0.0053
Total	561	600	30.5	34.7				

Notes: The table includes only stems $\geq$ 10 cm dbh and species that occurred in more than two stands. Paired *t* tests compare the relative basal area of each species between adjacent primary and secondary forests.

used (latitude and longitude, slope, aspect, and elevation). A single observer analyzed all images to minimize error in threshold determination. For each stand, we calculated the mean amount of radiation transmitted to the understory ($\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$) and the coefficient of variation among the 20 measures.

Ordinations

We described patterns of tree community composition with nonmetric multidimensional scaling (NMS) ordination using PC-ORD (McCune and Mefford 1999). NMS is theoretically preferable to other ordination methods (McCune and Grace 2002), though in this case, detrended correspondence analysis gave similar results. The ordination used Sørensen (Bray-Curtis) measures of community dissimilarity based on species' relative basal areas, including only species that occurred in >2 stands (i.e., >1 pair). Since it represents relative basal area, the ordination describes vegetation composition independent of its structure. Following McCune and Grace (2002), we first compared 40 iterations with real data and 50 iterations with randomized data to select an appropriate number of dimensions (axes). Then we performed 400 iterations with the chosen dimensionality to find a stable solution with minimal stress.

To summarize variation in the many interrelated soil chemical properties we measured, we conducted a principal-components analysis (PCA; PROC FACTOR in SAS). All variables except pH, Al, and Fe were first natural-log transformed to improve normality.

For both ordinations, we rotated the solution with the varimax method, which maximizes the variance of the factor loadings, and we interpreted the axes by calculating Pearson correlations with the original variables.

Statistical analyses

We assessed the effects of agricultural history on vegetation, soils, and light availability with analyses of variance (ANOVA; PROC GLM in SAS). First, multivariate tests evaluated overall effects on tree species composition (NMS axes) and soil chemical properties (PCA axes). Where primary and secondary forests differed overall, we proceeded to specify these differences with univariate analyses of variance. In all analyses, the response variables were the differences between the primary and secondary forests at each site, so the intercept term tested the effect of history. This design enabled us to perform multivariate ANOVAs that accounted for the pairing between stands. For univariate tests, it is equivalent to a paired *t* test or a mixed model with site as a random factor. Since we hypothesized that any effect of history on understory light levels would be mediated by changes in the forest canopy, we also evaluated the dependence of light availability on vegetation structure and composition. This analysis used a mixed model with site as a random factor. We tested all pairwise interactions and dropped nonsignificant terms sequentially.

RESULTS

Tree communities

Primary and secondary forests had a similar stem density, about 580 trees/ha ($F_{1,19} = 0.47$, $P = 0.5012$; Table 1). Tree size distributions also appeared similar in the two forest types, though secondary forests had more trees of 30–40 cm dbh (Fig. 1). Secondary forests had basal areas 14% greater, on average, than adjacent primary stands ($F_{1,19} = 5.21$, $P = 0.0341$; Table 1).

NMS ordination yielded a three-dimensional solution that explained 89% of the variation in tree species

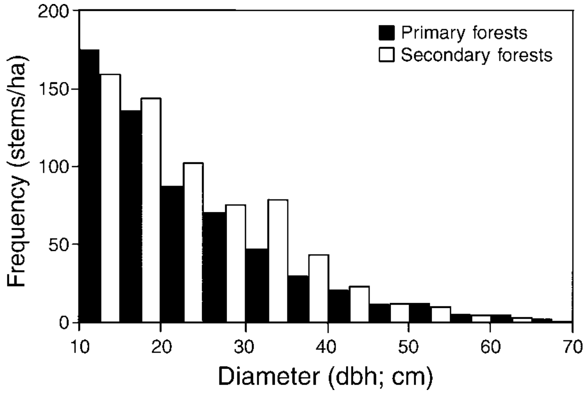

FIG. 1. Tree size distributions of primary forests and secondary forests in central New York (dbh $\geq$ 10 cm; five trees with dbh $>$ 70 cm are not shown).

composition. High scores on the first axis, which explained 42% of the variation, indicated dominance by *Acer saccharum* ($r = 0.90$) rather than *Acer rubrum* ($r = -0.72$; Fig. 2a). The second axis, explaining 23% of the variation, described a gradient from *Pinus strobus* ($r = 0.63$) to *Fagus grandifolia* ($r = -0.76$) and *Tsuga canadensis* dominance ($r = -0.50$). Axis 3 primarily represented *Acer rubrum* ($r = 0.69$) vs. *Fraxinus americana* ($r = -0.63$) and *Carya cordiformis* ($r = -0.57$).

Species composition of primary and secondary forests differed markedly overall ($F_{3,17} = 48.3$, $P < 0.0001$). Primary and secondary forests separated along both the first ($F_{1,19} = 44.3$, $P < 0.0001$) and second axes ($F_{1,19} = 52.5$, $P < 0.0001$), though not the third ($F_{1,19} = 0.06$, $P = 0.8123$). Relative to the adjacent primary stands, all 20 secondary forests shifted lower on Axis 1 and higher on Axis 2 (Fig. 2b).

The distinctness of primary and secondary forest communities resulted from differential distributions of many individual species. Primary forests were dominated by *Acer saccharum* (26% of total basal area), with *Fagus grandifolia* (17%), *Acer rubrum* (14%), and *Tsuga canadensis* (10%), whereas *Acer rubrum* and *Pinus strobus* together represented over half of the basal area in secondary stands (Table 1). Several species common in primary forests were almost completely absent from secondary stands, including *Fagus grandifolia*, *Tsuga canadensis,* and *Tilia americana* (see Plate 1).

Soil physical properties

Soil physical properties showed no consistent differences between forest types (Table 2). While soil water contents were similar between adjacent primary and secondary forests, they were more variable within stands of primary forest ($F_{1,19} = 23.8$, $P = 0.0001$; Fig. 3).

Primary and secondary forests also had similar levels of earthworm activity. Most sites had at least some earthworms present; only 5 of the 20 sites were completely free of worms. Earthworm activity was associated with increased bulk density ($r = 0.3969$, $P = 0.0112$) and reduced humus depth ($r = -0.7977$, $P < 0.0001$) and litter quantity ($r = -0.3461$, $P = 0.0287$). In fact, 85% of the pits with worms had no humus layer.

Soil chemical properties

Two main gradients in soil chemical properties emerged from the PCA. The first axis represented a pH gradient ($r = 0.94$) that was also associated with Ca ($r = 0.93$) and Mg ($r = 0.93$), which explained 42% of the variation (Fig. 4a). The second axis correlated most strongly with C ($r = 0.93$), organic matter (OM; $r = 0.88$), and N ($r = 0.84$), and it explained another 27% of the variation. Since these axes have clear interpretations, we refer to them as pH and OM axes, respectively.

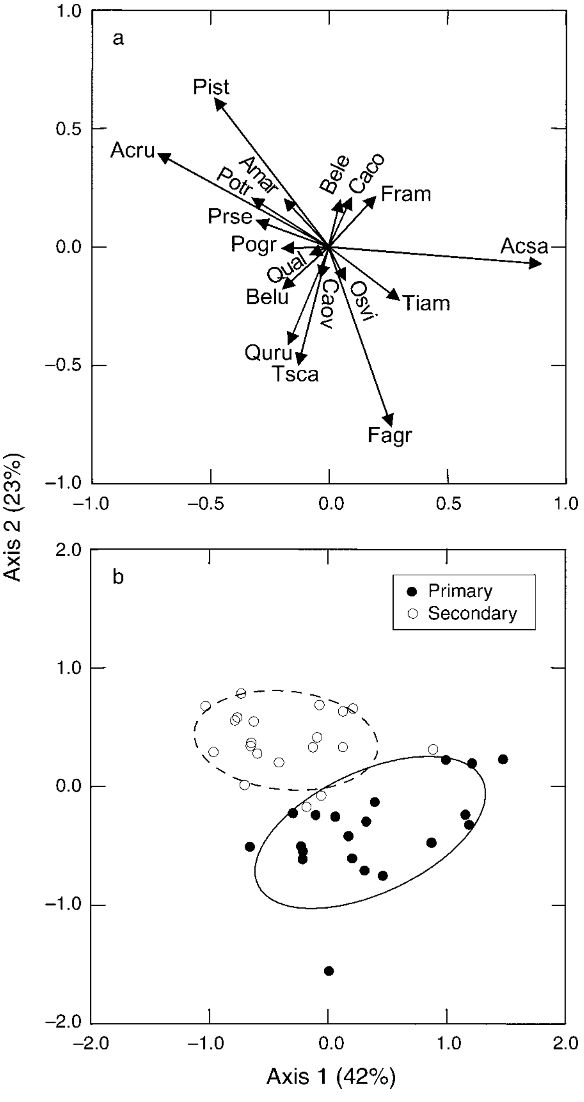

FIG. 2. NMS ordination of tree species composition. (a) A joint plot shows Pearson correlations between the axes and the species. Species abbreviations are the first two letters of the genus and species names (listed in Table 1). (b) A scatter plot of the sites has 68% confidence ellipses for primary forests (solid line) and secondary forests (dashed line). The third axis is not shown.

TABLE 2. Physical and chemical properties of primary and secondary forest soils (top 10 cm; mean ± SE; $N = 20$ forests of each type).

	Units	Primary forests	Secondary forests	t	P
Physical properties					
Whole-soil bulk density	g/cm^3	0.92 ± 0.04	0.97 ± 0.04	−1.36	0.1896
Coarse fragment concentration	cm^3/cm^3	0.11 ± 0.02	0.12 ± 0.01	−1.52	0.1461
Fine-earth bulk density	g/cm^3	0.72 ± 0.03	0.75 ± 0.04	−0.68	0.5058
Water content	cm^3/cm^3	0.41 ± 0.02	0.37 ± 0.02	1.48	0.1554
Humus depth (Oe + Oa)	cm	1.97 ± 0.36	2.03 ± 0.39	−0.11	0.9119
Litter quantity (Oi)	g/m^2	511 ± 49	484 ± 45	0.34	0.7378
Chemical properties					
pH		4.68 ± 0.12	4.75 ± 0.14	−0.96	0.351
OM	kg/ha	103 000 ± 5910	87 300 ± 3460	2.64	0.0162
C	kg/ha	52 100 ± 2950	43 800 ± 1640	3.25	0.0042
N	kg/ha	3280 ± 224	2970 ± 161	1.65	0.1159
C:N	kg/kg	16.3 ± 0.67	15.2 ± 0.56	2.04	0.055
P	kg/ha	3.9 ± 0.58	2.7 ± 0.40	2.31	0.032
K	kg/ha	75 ± 4.2	77 ± 4.8	−0.59	0.5654
Ca	kg/ha	976 ± 227	842 ± 205	1.11	0.2829
Mg	kg/ha	129 ± 23	115 ± 21	0.83	0.4191
Al	kg/ha	214 ± 25	198 ± 18	0.99	0.3351
Fe	kg/ha	101 ± 15	57 ± 5.2	3.74	0.0014
Cu	kg/ha	1.4 ± 0.23	1.2 ± 0.21	0.98	0.3378
Mn	kg/ha	89 ± 10	70 ± 4.9	1.9	0.0731
Zn	kg/ha	2.8 ± 0.21	2.6 ± 0.20	0.82	0.4227

Notes: For OM, C, and N, measurements represent total contents, whereas for all other nutrients they are extractable concentrations. Paired t tests indicate whether properties differ between adjacent primary and secondary forests.

Primary and secondary forest soils were somewhat different overall in chemical properties ($F_{2,18} = 4.50$, $P = 0.0260$). They overlapped completely on the pH axis ($F_{1,19} = 0.83$, $P = 0.3745$; Fig. 4b), and the pH of composite samples from adjacent pairs was similar (Table 2). However, within-stand variability in pH was greater in primary forests than in secondary ($F_{1,19} = 21.3$, $P = 0.0002$; Fig. 3). The OM axis separated paired forests of different history ($F_{1,19} = 9.30$, $P = 0.0066$; Fig. 4b), with secondary forest soils having on average 15% less OM than adjacent primary stands (Table 2). Total soil C averaged 16% lower in secondary forests, and extractable P was 29% lower (Table 2). Still, most secondary forests fell within the range spanned by primary forests along the OM axis, which exceeded any differences between paired stands (Fig. 4b).

Light availability

Understory light levels in primary and secondary forests were similar both in means ($F_{1,19} = 0.31$, $P =$

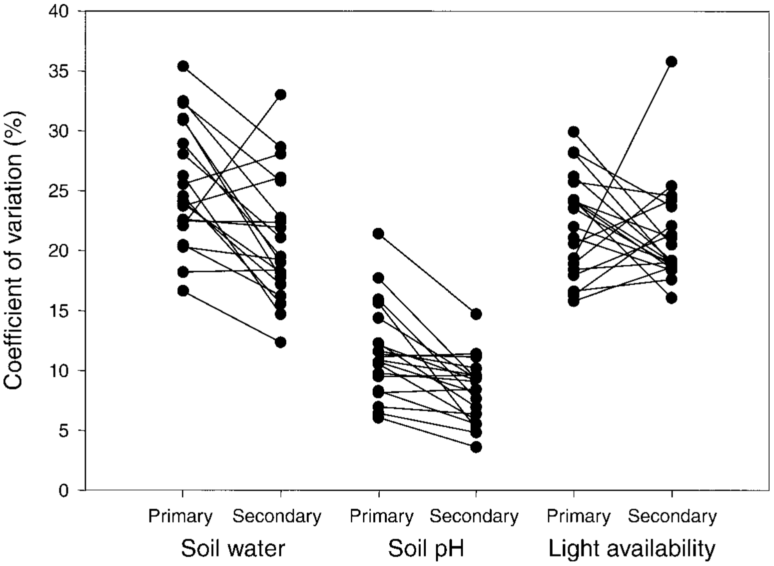

FIG. 3. Within-stand variability in soil water content, pH, and light availability, showing coefficients of variation for primary and secondary forests. Lines connect adjacent, paired stands.

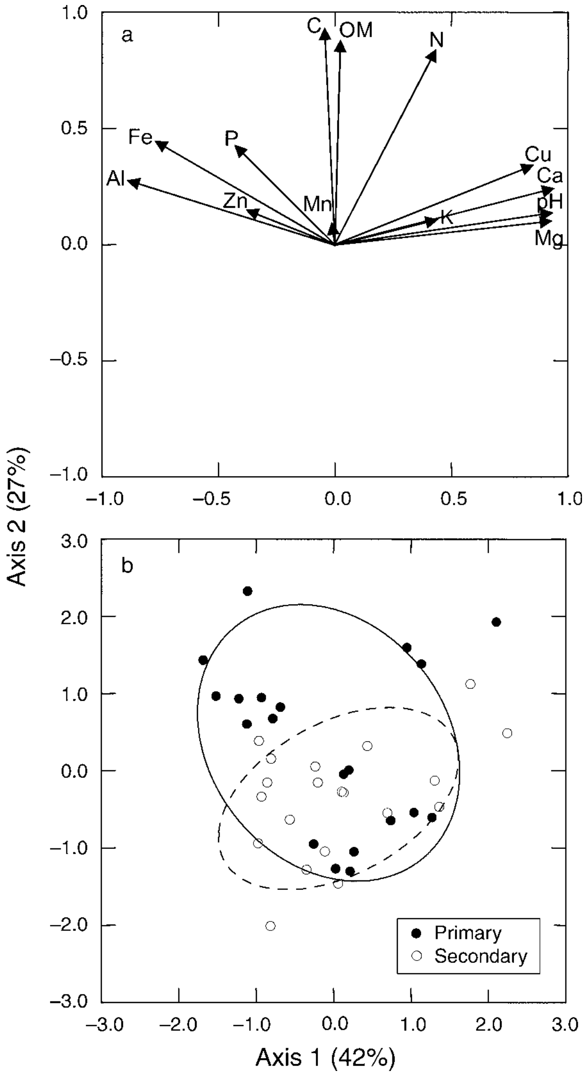

FIG. 4. Chemical properties of forest soils summarized by PCA, with (a) correlations between the axes and the measured variables and (b) confidence ellipses for primary and secondary forests, as in Fig. 2.

0.5813) and coefficients of variation ($F_{1,19} = 0.69$, $P = 0.4159$; Fig. 3). Primary forest floors received a mean of 6.67 ± 0.29 mol·m^{-2}·d^{-1}, and secondary forests 6.47 ± 0.23 mol·m^{-2}·d^{-1}. Light availability in the understory depended primarily on tree species composition; for example, stands with high proportions of *Fagus grandifolia* and *Tsuga canadensis* (i.e., low scores on the second vegetation axis) had lower understory light levels (Table 3).

DISCUSSION

While agriculture had lasting effects on vegetation and soils in central New York forests, environmental conditions in forests on former agricultural lands also show a substantial degree of recovery. In 100 years, previously plowed fields have developed many attributes indistinguishable from adjacent forests that were never cleared. Trees in post-agricultural stands have reached a density and size distribution comparable to uncleared forests and surpassed them in total basal area. This similarity in canopy structure apparently produces similar light regimes in the forest understories. Previously plowed soils have regained the characteristics of soils in uncleared forests in all of the physical properties and many of the chemical properties we measured. In particular, agriculture had no detectable effect on soil properties associated with pH, a principal control on soil fertility and a dominant gradient of environmental variation across the landscape.

Present environmental conditions may have converged in part because intervening disturbances and shifts in species composition now exert a stronger influence than more distant history. For example, periodic, selective harvesting has reduced the stem density and basal area of almost all primary forests in the region, making them more similar to the developing stands. Neither forest type in this study has the structural characteristics of the old-growth stands they replaced, which would likely have supported similar total basal areas (about 30 m^2/ha) but fewer, larger trees (about 400 stems/ha ≥10 cm dbh; Keddy and Drummond 1996, McGee et al. 1999). Another factor likely to have facilitated the rapid recovery of basal area in post-agricultural forests is their species composition. Post-agricultural forests had a greater abundance of tree species that tend to attain disproportionately large diameters for their age and height, especially when open-grown, such as *Pinus strobus, Fraxinus americana,* and the *Populus* species.

Dominance by *Pinus strobus* probably contributed to the development of post-agricultural forest floors as well, since conifers tend to accumulate thicker, more massive litter and humus layers than hardwood stands (Lutz and Chandler 1946). Similar forest floors in the two forest types may also result from similar levels of earthworm activity. Exotic earthworms now occur throughout adjacent forests regardless of past land-use boundaries, and they may have a dominant impact on forest-floor characteristics. In particular, the increased bulk density and reduced humus depth and litter

TABLE 3. Mixed model showing the effects of agricultural history, vegetation structure, and composition on understory light availability.

Effect	Direction	df	Type III SS	*F*	*P*
Agricultural history	−	1	2.02	3.19	0.0929
Basal area	−	1	1.57	2.49	0.134
Vegetation Axis 2	+	1	3.45	5.47	0.0327
Vegetation Axis 3	−	1	4.6	7.28	0.0158

Notes: The dependent variable is the amount of radiation transmitted to the understory (mol·m^{-2}·d^{-1}). The model explains 80% of the variation in light availability. The random effect of site is not shown.

PLATE 1. (Left) A primary forest in central New York. In late fall, tree shadows highlight the distinctive microtopography created by treefall pits and mounds. The presence of *Fagus grandifolia* and *Tsuga canadensis* is also typical of primary forests on the region's mesic uplands. Photo credit: S. Gardescu. (Right) In contrast, this secondary forest on previously plowed land has a smooth forest floor and a tree community dominated by *Acer rubrum*. Photo credit: P. L. Marks.

quantity seen here in stands with more earthworm activity are consistent with results from nearby sites, where earthworm introduction eliminated forest-floor organic horizons, decreased surface-soil organic matter storage by 30%, and doubled rates of litter disappearance (Bohlen et al. 2004, Suárez et al. 2006).

The most striking legacy of agriculture in central New York forests is the change in tree species composition. As in many other landscapes, past land use still controls much of the variation in present vegetation (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1996, Dupouey et al. 2002). Tree species distributions across habitats of different history followed long-known patterns. By 1860, Thoreau (1993) recognized *Acer rubrum* and *Pinus strobus* as common invaders of cleared and cultivated lands in southern New England. These species have since been seen to dominate post-agricultural communities across the northeastern United States, whereas *Fagus grandifolia* and *Tsuga canadensis* have been notably slow to colonize abandoned agricultural lands (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1999, Mohler et al. 2006). Selective logging of the primary stands may have enhanced their distinctness from post-agricultural forests by reducing the abundance of *Pinus strobus* and the *Quercus* species and reinforcing the dominance of *Fagus grandifolia*, which has no commercial value. As a result of their different disturbance histories, tree communities in the two forest types had entirely distinct compositions (Fig. 2b), indicating that agriculture has created plant communities with novel combinations and relative abundances of species.

Historical agriculture also caused persistent reductions in surface-soil OM, C, and P contents. If cultivation reduced soil C by 30% (Johnson 1992, Davidson and Ackerman 1993, Murty et al. 2002), then post-agricultural forest soils have so far regained about half of the amount they lost. A deficit of this magnitude is still larger than the small and variable, usually <10%, changes in soil OM and C caused by forest harvesting alone (including the experimental, whole-tree clearcut at Hubbard Brook; Johnson et al. 1991, Johnson 1992). Many other studies have likewise found that soil OM and C continue to accumulate on formerly cultivated lands for as many as 100 years (Billings 1938, Thorne and Hamburg 1985, Richter et al. 1994, Hooker and Compton 2003). In this study, however, soil OM in post-agricultural forests generally remained within the range of uncleared forests (Fig. 4b). Though lower than in adjacent unplowed soils, OM levels in previously plowed soils were comparable to amounts found in many other unplowed soils across the landscape.

The reduced P in post-agricultural forest soils in central New York contrasts with several findings that soils remain enriched in P hundreds of years after abandonment from agriculture, evidently due to organic amendments (Koerner et al. 1997, Compton and Boone 2000, Dupouey et al. 2002, De Keersmaeker et al. 2004). Given that P increases from manuring can persist for at least 100 years (as in the long-term field experiments at Rothamsted Experimental Station, Harpenden, Hertfordshire, UK; Catt 1994), and that comparable central New York soils show lasting P enrichment where animal densities were high, such as in former barnyards (E. L. Stone, *personal communication*), this result suggests that manure additions must have been small or absent in the former plowed fields we studied. Rather, removing vegetation and harvesting crops would have reduced P inputs to the soil, and the physical mixing of soil horizons by plowing may have accelerated the cycling and leaching of otherwise relatively immobile P.

Erosion could also account for the losses of OM, C, and P. Though rocks would have been removed from plowed fields, coarse fragment concentrations were slightly but not significantly higher in post-agricultural soils, suggesting that some erosion of fine soil may have occurred. If so, soil from the more OM- and nutrient-rich surface layers would have been lost, and deeper, less rich layers exposed. It is also possible that plowing redistributed fine soil in situ, shifting OM, C, and P to deeper soil horizons (Motzkin et al. 1996). A full account of land-use impacts on soil OM and nutrient contents would require deeper sampling, as well as measurements of nutrient transformation rates. But regardless of their cause, the lower OM and nutrient levels we observed in surface soils could hinder the growth and survival of some herbaceous plants and tree seedlings in post-agricultural forests.

Another important legacy of cultivation is the spatial homogenization of soil properties. The reduced within-stand variability in the pH and water content of post-agricultural forest soils corroborates previous observations that cultivation homogenizes soil pH and other properties (Wilson et al. 1997, De Keersmaeker et al. 2004, Fraterrigo et al. 2005). Though not unexpected, given the mechanical soil mixing inherent in plowing and the uniform litter inputs from crop monocultures, this consistent result has often been overlooked in studies that rely on composite samples or focus on mean resource supply. Reductions in small-scale heterogeneity have potentially large biological significance for understory plant communities. Altered patterns of resource availability can affect population structure, diversity, and community composition by changing the performance of individual species and the outcome of competitive interactions (Beckage and Clark 2003, Day et al. 2003, Hutchings et al. 2003). For example, the more homogeneous environments in post-agricultural forests could exclude species that require specific regeneration niches or depend on resource-poor patches as refuges from competition.

Implications for understory plant communities

Environmental features other than those we considered may well be critical to certain species. The importance of the biotic environment, such as interactions with mycorrhizae, herbivores, pollinators, and pathogens, also remains an open question (Flinn and Vellend 2005). But to the extent that we measured relevant environmental gradients, the results of this study suggest that agricultural legacies in forest environments may play an important role in plant community recovery. Since the ranges of environmental conditions within the two forest types broadly overlap, plants could experience the same levels of light, water, and nutrient availability in either post-agricultural or uncleared forests across the central New York landscape. The environmental differences we observed would thus be insufficient to explain a species' exclusion from one of the forest types. However, the lasting soil OM, C, and P depletion and the elimination of extreme microsites in post-agricultural forests could contribute to reductions in the frequency and performance of some species and the diversity of understory communities.

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LITERATURE CITED

Ball, D. F. 1964. Loss-on-ignition as an estimate of organic matter and organic carbon in non-calcareous soils. Journal of Soil Science 15:84–92.

Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65:1406–1419.

Beckage, B., and J. S. Clark. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. Ecology 84:1849–1861.

Billings, W. D. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. Ecological Monographs 8:437–499.

Bohlen, P. J., D. M. Pelletier, P. M. Groffman, T. J. Fahey, and M. C. Fisk. 2004. Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests. Ecosystems 7:13–27.

Bossuyt, B., M. Hermy, and J. Deckers. 1999. Migration of herbaceous plant species across ancient–recent forest ecotones in central Belgium. Journal of Ecology 87:628–638.

Braun, E. L. 1950. Deciduous forest of eastern North America. Hafner Press, New York, New York, USA.

Catt, J. A. 1994. Long-term consequences of using artificial and organic fertilisers: the Rothamsted experiments. Pages 119–134 *in* S. Foster and T. C. Smout, editors. The history of soils and field systems. Scottish Cultural Press, Aberdeen, UK.

Compton, J. E., and R. D. Boone. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81:2314–2330.

Compton, J. E., R. D. Boone, G. Motzkin, and D. R. Foster. 1998. Soil carbon and nitrogen in a pine–oak sand plain in central Massachusetts: role of vegetation and land-use history. Oecologia 116:536–542.

Davidson, E. A., and I. L. Ackerman. 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. Biogeochemistry 20:161–193.

Day, K. J., M. J. Hutchings, and E. A. John. 2003. The effects of spatial pattern of nutrient supply on yield, structure and mortality in plant populations. Journal of Ecology 91:541–553.

De Keersmaeker, L., L. Martens, K. Verheyen, M. Hermy, A. De Schrijver, and N. Lust. 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). Forest Ecology and Management 188:291–304.

Dupouey, J. L., E. Dambrine, J. D. Laffite, and C. Moares. 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83:2978–2984.

Dzwonko, Z. 2001. Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. Journal of Applied Ecology 38:942–951.

Dzwonko, Z., and S. Loster. 1989. Distribution of vascular plant species in small woodlands on the Western Carpathian foothills. Oikos 56:77–86.

Ehrlén, J., and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. Ecology 81:1667–1674.

Federer, C. A., D. E. Turcotte, and C. T. Smith. 1993. The organic fraction–bulk density relationship and the expression of nutrient content in forest soils. Canadian Journal of Forest Research 23:1026–1032.

Flinn, K. M., and P. L. Marks. 2004. Land-use history and forest herb diversity in Tompkins County, New York, USA. Pages 81–95 *in* O. Honnay, K. Verheyen, B. Bossuyt, and M. Hermy, editors. Forest biodiversity: lessons from history for conservation. CABI, Wallingford, UK.

Flinn, K. M., and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3:243–250.

Flinn, K. M., M. Vellend, and P. L. Marks. 2005. Environmental causes and consequences of forest clearance and agricultural abandonment in central New York. Journal of Biogeography 32:439–452.

Foster, D. R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. Journal of Ecology 80:753–772.

Fraterrigo, J. M., M. G. Turner, S. M. Pearson, and P. Dixon. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. Ecological Monographs 75:215–230.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Users manual and program documentation. Version 2.0. Simon Fraser University, Burnaby, British Columbia, Canada and the Institute of Ecosystem Studies, Millbrook, New York, USA.

Glitzenstein, J. S., C. D. Canham, M. J. McDonnell, and D. R. Streng. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. Bulletin of the Torrey Botanical Club 117:106–122.

Graae, B. J., P. B. Sunde, and B. Fritzbøger. 2003. Vegetation and soil differences in ancient opposed to new forests. Forest Ecology and Management 177:179–190.

Grossman, R. B., and T. G. Reinsch. 2002. Bulk density and linear extensibility. Pages 201–228 *in* J. H. Dane and G. C. Topp, editors. Methods of soil analysis. Part 4: physical methods. Soil Science Society of America, Madison, Wisconsin, USA.

Hooker, T. D., and J. E. Compton. 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecological Applications 13: 299–313.

Hutchings, M. J., E. A. John, and D. K. Wijesinghe. 2003. Toward understanding the consequences of soil heterogeneity for plant populations and communities. Ecology 84:2322–2334.

Johnson, C. E., A. H. Johnson, T. G. Huntington, and T. G. Siccama. 1991. Whole-tree clear-cutting effects on soil horizons and organic-matter pools. Soil Science Society of America Journal 55:497–502.

Johnson, D. W. 1992. Effects of forest management on soil carbon storage. Water, Air, and Soil Pollution 64:83–120.

Kalisz, P. J. 1986. Soil properties of steep Appalachian old fields. Ecology 67:1011–1023.

Keddy, P. A., and C. G. Drummond. 1996. Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. Ecological Applications 6:748–762.

Koerner, W., J. L. Dupouey, E. Dambrine, and M. Benoît. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. Journal of Ecology 85:351–358.

Lewis, A. B. 1934. An economic study of land utilization in Tompkins County, New York. Cornell University Agricultural Experiment Station Bulletin 590. Ithaca, New York, USA.

Lutz, H. J., and R. F. Chandler, Jr.. 1946. Forest soils. John Wiley and Sons, New York, New York, USA.

Marks, P. L., and S. Gardescu. 1992. Vegetation of the central Finger Lakes region of New York in the 1790s. Pages 1–35 *in* Late eighteenth century vegetation of Central and Western New York State on the basis of original land survey records. New York State Museum Bulletin 484. Albany, New York, USA.

Marks, P. L., and S. Gardescu. 2001. Inferring forest stand history from observational field evidence. Pages 177–198 *in* D. Egan and E. A. Howell, editors. The historical ecology handbook: a restorationist's guide to reference ecosystems. Island Press, Washington, D.C., USA.

Matlack, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75:1491–1502.

Matlack, G. R. 1997. Land use and forest habitat distribution in the hinterland of a large city. Journal of Biogeography 24: 297–307.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., and M. J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data, Version 4.25. MjM Software Design, Gleneden Beach, Oregon, USA.

McGee, G. G., D. J. Leopold, and R. D. Nyland. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. Ecological Applications 9:1316–1329.

Mohler, C. L., P. L. Marks, and S. Gardescu. 2006. Guide to the plant communities of the central Finger Lakes region. New York State Agricultural Experiment Station, Geneva, New York, USA.

Morgan, M. F. 1941. Chemical soil diagnosis by the universal soil testing system. Connecticut Agricultural Experiment Station Bulletin 450. New Haven, Connecticut, USA.

Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecological Monographs 66: 345–365.

Motzkin, G., P. Wilson, D. R. Foster, and A. Allen. 1999. Vegetation patterns in heterogeneous landscapes: the importance of history and environment. Journal of Vegetation Science 10:903–920.

Murty, D., M. U. F. Kirschbaum, R. E. McMurtrie, and H. McGilvray. 2002. Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. Global Change Biology 8:105–123.

Neeley, J. A. 1965. Soil survey: Tompkins County, New York. Series 1961, number 25. United States Department of Agriculture, Soil Conservation Service, Government Printing Office, Washington, D.C., USA.

Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter. Pages 961–1010 *in* D. L. Sparks, editor. Methods of soil analysis, part 3: chemical methods. Soil Science Society of America, Madison, Wisconsin, USA.

Northeast Regional Climate Center. 2005. The climate of Ithaca, NY. Cornell University, Ithaca, New York, USA. ⟨http://www.nrcc.cornell.edu/climate/ithaca/normal.html⟩

Page-Dumroese, D. S., M. F. Jurgensen, R. E. Brown, and G. D. Mroz. 1999. Comparison of methods for determining bulk densities of rocky forest soils. Soil Science Society of America Journal 63:379–383.

Peterken, G. F. 1981. Woodland conservation and management. Chapman and Hall, London, UK.

Peterken, G. F., and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. Journal of Ecology 72:155–182.

Post, W. M., and L. K. Mann. 1990. Changes in soil organic carbon and nitrogen as a result of cultivation. Pages 401–407 *in* A. F. Bouwman, editor. Soils and the greenhouse effect. John Wiley and Sons, New York, New York, USA.

Rackham, O. 1980. Ancient woodland: its history, vegetation and uses in England. E. Arnold, London, UK.

Rackham, O. 1986. The history of the countryside. J. M. Dent, London, UK.

Rhoads, A. G., S. P. Hamburg, T. J. Fahey, T. G. Siccama, and R. Kobe. 2004. Comparing direct and indirect methods of assessing canopy structure in a northern hardwood forest. Canadian Journal of Forest Research 34:584–591.

Richter, D. D., D. Markewitz, C. G. Wells, H. L. Allen, R. April, P. R. Heine, and B. Urrego. 1994. Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. Ecology 75:1463–1473.

Singleton, R., S. Gardescu, P. L. Marks, and M. A. Geber. 2001. Forest herb colonization of post-agricultural forests in central New York State, USA. Journal of Ecology 89:325–338.

Smith, B. E., P. L. Marks, and S. Gardescu. 1993. Two hundred years of forest cover changes in Tompkins County, New York. Bulletin of the Torrey Botanical Club 120:229–247.

Suárez, E. R., T. J. Fahey, J. B. Yavitt, P. M. Groffman, and P. J. Bohlen. 2006. Patterns of litter disappearance in a northern hardwood forest invaded by exotic earthworms. Ecological Applications 16:154–165.

Thoreau, H. D. 1993. The dispersion of seeds. Pages 23–173 *in* B. P. Dean, editor. Faith in a seed: the dispersion of seeds and other late natural history writings. Island Press, Washington, D.C., USA.

Thorne, J. F., and S. P. Hamburg. 1985. Nitrification potentials of an old-field chronosequence in Campton, New Hampshire. Ecology 66:1333–1338.

Vaughan, L. M. 1928. Abandoned farm areas in southern New York. Dissertation. Cornell University, Ithaca, New York, USA.

Vellend, M. 2003. Habitat loss inhibits recovery of plant diversity as forests regrow. Ecology 84:1158–1164.

Vellend, M. 2004. Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. Ecology 85: 3043–3055.

Verheyen, K., B. Bossuyt, M. Hermy, and G. Tack. 1999. The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. Journal of Biogeography 26:1115–1128.

Walrath, F. J. 1927. A history of the agriculture of Tompkins County, New York. Dissertation. Cornell University, Ithaca, New York, USA.

Williams, M. 1989. Americans and their forests: a historical geography. Cambridge University Press, New York, New York, USA.

Wilson, B. R., A. J. Moffat, and S. Nortcliff. 1997. The nature of three ancient woodland soils in southern England. Journal of Biogeography 24:633–646.

APPENDIX

Site characteristics of primary and secondary forests in central New York, including latitude, longitude, elevation, slope, aspect, and soil type (*Ecological Archives* A017-017-A1).