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Legacies of land use history diminish over 22 years in a forest in southeastern New York[1,2]

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Katz, D. S. W. (Environmental Studies Program, Bard College, Annandale, NY 12504), G. M. Lovett, C. D. Canham (Cary Institute of Ecosystem Studies, Millbrook, NY 12545), and C. M. O'Reilly (Biology Program, Bard College, Annandale, NY 12504). Legacies of land use history diminish over 22 years in a forest in southeastern New York. J. Torrey Bot. Soc. 137: 236–251. 2010.— Historical land use has shaped ecosystem structure and function in much of eastern North America, but the question of how long the legacies of 19th and 20th century agriculture will persist in forested landscapes remains a matter of debate. To evaluate whether the legacies of land use are diminishing over time we resampled permanent vegetation plots in areas which either did or did not have an agricultural history. This study focused on changes in trees, shrubs, herbaceous plants, and soil chemistry between 1984 and 2006 at the Cary Institute of Ecosystem Studies in southeastern New York State.

Substantial shifts in tree species composition were observed, including a decline in the basal area of *Cornus florida* and *Quercus prinus*. These changes appear to be due, respectively, to dogwood anthracnose and mortality associated with gypsy moth (*Lymantria dispar*) defoliation. *Quercus rubra* and *Acer saccharum* increased in basal area over the same period. Sapling density in the plots remained nearly constant between 1984 and 2006, but seedling density nearly doubled. The invasive herbaceous plant *Alliaria petiolata* increased markedly in percent cover and frequency of occurrence. *Acer rubrum* and *Q. prinus* tree abundances were highly correlated with land use history, while *A. saccharum* and *Q. rubra* were not, so the documented changes in forest composition have obscured some of the legacies of land use history on this forest over the past two decades. In addition to the changes caused by novel pests and pathogens, we show how other regional influences on forests (such as fire suppression and invasive plants) may diminish the differences in forest composition between forests with and without agricultural history.

Key words: *Alliaria petiolata*, disturbance, forest change, invasive species, land use history, *Lymantria dispar*, *Quercus prinus*, succession, *Tsuga canadensis*.

Much of the current forest area of the northeastern U.S. is undergoing succession following colonization of abandoned agricultural land. Even in forests that have not been actively managed since agricultural abandonment, land use history remains a major determinant of forest composition and structure (Glitzenstein et al. 1990, Bellemare et al. 2002, Foster and Aber 2004, Goslee et al. 2005, Flinn and Marks 2007). However, it is unknown whether the associations of particular forest types with specific land use histories (e.g., whether the land was used for agriculture or as a woodlot during the 19th and 20th century) will diminish over time or be amplified as forests with different land use histories develop in novel directions (Rhemtulla et al. 2009). If forests occupying former agricultural land become more similar to forests on land not used for agriculture, the legacy of land use history will be reduced.

While some have predicted that species composition in forests with different land use histories will become more similar as succession occurs in post-agricultural forests (Christensen and Peet 1984, Franklin et al. 1993),

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other researchers remain skeptical that succession will erase differences in species composition between forests with different histories in the foreseeable future (Glitzenstein et al. 1990, Foster et al. 2003). However, forests are changing for reasons other than succession. During the last century forests in the Northeast have been subject to a wide range of anthropogenic influences, including novel pathogens, exotic insects, invasive plants, climate change, fragmentation, fire prevention, and atmospheric deposition (Cronon 1983, Foster et al. 1992, Foster and Aber 2004, Lovett et al. 2006). These, and other disturbances, can either impact forest composition regardless of land use history or can disproportionately affect forests with specific land use histories. Whether the legacies of land use history will diminish over time therefore depends not just on succession but also on the strength of these other forces.

Empirical studies of forest dynamics have often been conducted with chronosequences, but this approach is not well-suited for untangling how non-successional forces may affect the legacies of land use. Chronosequences, which rely upon quantifying the degree of similarity in vegetation composition between forests that have been growing for different amounts of time after agricultural abandonment, also make the often untenable assumptions that each site differs only in age and is following the same general successional course (Johnson and Miyanishi 2008). Other studies which simply look at differences between forests with different histories are important, but offer little insight into how these patterns may change in the future (Glitzenstein et al. 1990, Gerhardt and Foster 2002).

In contrast, decade-scale studies can provide a more detailed picture of how a forest has changed, and, when combined with information on potential drivers of change, can lead to inferences about the causes of the observed dynamics and future directions of forest development (e.g., Hemond et al. 1983, Lorimer 1984, Fain et al. 1994, Galbraith and Martin 2005, Runkle et al. 2005, Ozier et al. 2006, Weckel et al. 2006, Schuster et al. 2008). Even more valuable are studies that quantify multiple aspects of forested ecosystems such as overstory, understory, herbaceous plants, and soil chemistry (Greller et al. 1990, Woods 2000, Goslee et al. 2005), allowing for a more complete understanding of changes and deeper insights into the dynamics between different subsystems.

The purpose of this study was to investigate how disturbances, successional processes, and the other forces which are impacting Northeastern forests have influenced the legacies of land use history over the last two decades. To do so, we quantified the changes over 22 years in forests near Millbrook, in the Hudson Valley of southeastern New York State. A vegetation survey conducted in 1984 reported the structure and composition of these same forests and revealed the relationship between forest composition and land-use history (Glitzenstein et al. 1990). The current study replicates the Glitzenstein et al. (1990) study 22 years later, in 2006, and evaluates shifts in trees, understory vegetation, and soil chemistry. Our study focuses on the following questions: 1) How have these forests changed over the past 22 years? 2) To what extent have forests with different land use histories become more similar or dissimilar and why? 3) How might this inform our predictions regarding the future persistence of the legacies of land use history in an era of global change?

Materials and Methods. Site Description. The research site was at the Cary Institute of Ecosystem Studies (CIES) in Dutchess County, New York (41° 50′ N, 73° 45′ W). About 325 ha of CIES property is forested, with the majority of wooded area located around the Canoo Hills and Teahouse Hill. The annual average temperature is 9.6 °C and precipitation averages 1110 mm yr^{-1}, with mean annual precipitation pH ranging from 4.0 to 4.4 between 1984 and 2004 (Kelly et al. 2006). The bedrock is mostly shale and slate and soils are predominantly thin and well-drained silt loams of the Nassau and Woodlawn series (Glitzenstein et al. 1990). The land was historically a patchwork of pasture and woodlot. Woodlots were selectively logged, but generally remained forested. Agriculture abandonment began in the 1890s, farming ceased entirely by 1939, and the forests have regrown from these pastures and woodlots without active management. Data collected by Glitzenstein et al. (1990) showed significant differences in forest composition between former woodlots and post-agricultural study plots in the Canoo Hills. In terms of tree species, the plot data from 1984 show that

Betula lenta L. (black birch) and *Fraxinus americana* L. (white ash) were more common in former agricultural areas and that *Quercus prinus* L. (chestnut oak) was more common in former woodlots (Glitzenstein et al. 1990). The gypsy moth (*Lymantria dispar*), an introduced defoliating insect, reached very high population levels and caused severe defoliation in 1980–1981 and to a lesser degree in 1989–1990 (Goodwin et al. 2005).

FIELD METHODS. A vegetation survey was carried out to replicate the work conducted by Glitzenstein et al. (1990). We sampled the same permanent plots that were established in 1984. Each circular plot had an area of 0.05 ha. The original stakes marking plot centers were relocated, allowing for a highly accurate resampling of each plot for a valid comparison of vegetation change over time (Loeb 1989). We sampled 43 of the original 46 plots in the Canoo Hills. Because we were unable to locate the center stakes for the remaining three plots we excluded them from this study. Additional data on 19 of the 43 plots were available from surveys of canopy condition conducted in 1993, 1997, and 2002. One aspect of these canopy surveys was to tag each individual tree in those 20 plots, allowing the life history of individual trees to be tracked.

Glitzenstein et al. (1990) thoroughly researched the land use history of the Canoo Hills by studying historical records and recording landscape clues such as stone walls, stumps, pit and mound topography, and soil profiles. Because the peak level of deforestation in this area occurred by 1890, they divided the landscape into areas that were either forested or not forested in 1890, with the assumption that if an area was forested then it was likely always to have been a woodlot. We used their classifications for the 43 plots that we resampled (21 of which were post-agricultural, 20 were former woodlots, and 2 plots had an unknown status; those two plots were excluded from our analyses).

A variety of measurements were taken at each plot, using similar methods to the original study (Glitzenstein et al. 1990). The diameter at breast height (DBH) of each standing tree (defined as stems $\geq$ 10 cm DBH) within the plot was measured, the species recorded, and a canopy class (understory, subcanopy, canopy, or dead) assigned. Although Glitzenstein et al. (1990) recorded crown dieback, we did not do so.

In two quarters of each plot all saplings (defined as $>$ 1 m in height and $<$ 10 cm DBH and belonging to a tree species) were identified, counted, and measured for DBH. In addition, eight rectangular (1 $\times$ 0.5 m) seedling and herbaceous plant quadrats were placed in each plot, along a transect running from east to west. In each quadrat the percent cover of each type of surface was recorded, including litter layer, exposed rock, dead wood, and a percent cover estimated for each species of herbaceous plant found within the quadrat. For practicality plants belonging to the genera *Rubus*, *Solidago*, and *Aster* as well as graminoids were recorded by genus only. Tree seedlings were identified and counted. Shrub cover in the plot was also recorded, based on cover along 20 m of the main east-west transect. Because Glitzenstein et al. (1990) had recorded which sections of the plot they measured for saplings and the distance along the transect that their quadrats were placed, our sapling and quadrat sampling was done in the exact same locations as the original sampling. In the 43 plots that were sampled, we measured 86 plot-quarters for saplings (covering 10,340 m^2) and 344 quadrats for seedlings and herbaceous plants (covering 172 m^2). To avoid seasonal differences, we sampled all plots within a month of the original sampling date and 77% of the plots were sampled within two weeks of the original date. Nomenclature follows Gleason and Cronquist (1991).

Following the procedure used by Glitzenstein et al. (1990), soil samples were taken from four randomly located points along the east-west transect in each plot. Each sample was taken from the top 10 cm of the mineral soil using a 2 cm diameter soil corer, and the depth of the organic layer was measured. The soil samples from each plot were composited in a resealable plastic bag and stored in a cold room until analysis. Soil samples were air dried for one week and sieved through a 2 mm screen. Soil pH was determined in a 1:1 slurry with de-ionized water using a dual pH electrode. The methods used to determine exchangeable cation concentrations in 2006 followed the original methods used in 1984 as closely as possible. 5.00 g of sieved soil was weighed into a beaker, and 50.0 mL of ammonium acetate (NH_4OAc; 1 M) was

Table 1. Changes in the basal area, density, and importance values of select tree species in 1984 and 2006. Basal area is in m^2 ha^{-1}, density is in stems ha^{-1}, and importance values are in percentages. P is the probability that 2006 values are significantly different from 1984 values according to paired t-tests, where * = $P < 0.05$. This table provides data on trees that were ≥10 cm DBH.

	Basal area			Density			Importance value		
Species	1984	2006	P	1984	2006	P	1984	2006	P
Quercus prinus	6.339	5.151	*	80.0	51.1	*	20.0	14.6	*
Quercus rubra	3.093	4.648	*	46.0	52.1	*	10.4	13.8	
Pinus strobus	2.520	3.084	*	50.2	43.0	*	9.6	10.0	
Acer rubrum	2.421	2.392		87.4	60.9	*	12.8	10.6	
Tsuga canadensis	2.405	2.979	*	58.6	66.5	*	10.2	12.2	
Other	1.720	1.528		57.3	39.9		8.7	6.9	
Acer saccharum	1.666	2.267	*	55.7	72.5	*	8.4	11.6	*
Carya glabra	1.666	1.691		43.0	34.8	*	7.2	6.6	
Betula lenta	1.015	1.231	*	26.6	25.6		4.5	4.8	
Quercus alba	0.837	1.051	*	14.3	13.3		3.0	3.3	
Quercus velutina	0.620	0.827	*	12.3	13.3		2.4	2.8	
Fraxinus americana	0.484	0.664	*	17.4	14.3	*	2.5	2.7	
Cornus florida	0.026	0.004	*	2.1	0.5	*	0.3	0.1	
Total	24.810	27.519		550.8	487.6		100	100	

added. These containers were shaken and left to settle overnight. The next day, the containers were shaken again and poured through Whatman #41 filters to remove particles. The beaker was rinsed with four rinses of 25.0 mL of NH_4OAc, which were also poured through the filter. After filtration, the extractant was refrigerated overnight and then analyzed for calcium (Ca) and magnesium (Mg) using a Leeman Labs Profile inductively coupled plasma emission spectrometer.

In addition, we had access to soil samples that were collected and analyzed in 1984. Dried samples had been stored in plastic bags in a dark cabinet over the 22-yr period. We used the same techniques to analyze 17 soil samples for the relevant cations, in order to control for possible differences in analytical equipment over the 22 years. The specific samples selected were chosen because they covered the range of cation concentrations and because sufficient soil had been archived. Additionally, we reanalyzed two samples from 2006 at the same time in order to control for possible differences between each batch.

Data Analysis. Basal area was calculated from DBH assuming a circular bole cross-section. Relative basal area was calculated as the basal area of a given species divided by the basal area of all species for that plot. Relative density was calculated similarly. Importance values were calculated as the average of relative basal area and relative density. Above-ground biomass was calculated for each tree (total above-ground biomass when available; otherwise total above-ground woody biomass), using the species and regional specific dimension analysis equations published by Ter-Mikaelian and Korzukhin (1997).

We used paired and unpaired t-tests to determine whether changes in specific variables were significant across all plots. Data were analyzed with SAS and JMP (SAS Institute, Cary, NC).

Results. Trees. We recorded a total of 1174 trees ≥ 10 cm DBH, which represented 24 tree species. Comparison with the original 1984 dataset revealed substantial changes in many species (Table 1). One of the most notable changes was a decline in *Quercus prinus* density by 36%. Intermediate data points from the canopy census show that the decline in *Q. prinus* happened rather rapidly between 1984 and 1993 (Fig. 1), when many tagged *Q. prinus* trees died. Other notable trends in density include a decline in *Cornus florida* L. (flowering dogwood) by 79% and increases in *Acer saccharum* Marsh. (sugar maple) by 30% and *Tsuga canadensis* L. Carr. (eastern hemlock) by 13%. Although the total basal area of the forest did not increase significantly between 1984 and 2006, total tree biomass increased significantly from 6976 kg ha^{-1} in 1984 to 8295 kg ha^{-1} in 2006 ($P < 0.001$). This reflects changes in tree diameter distributions (and corresponding nonlinear changes in individual tree biomass) that have occurred even though basal area has not changed significantly.

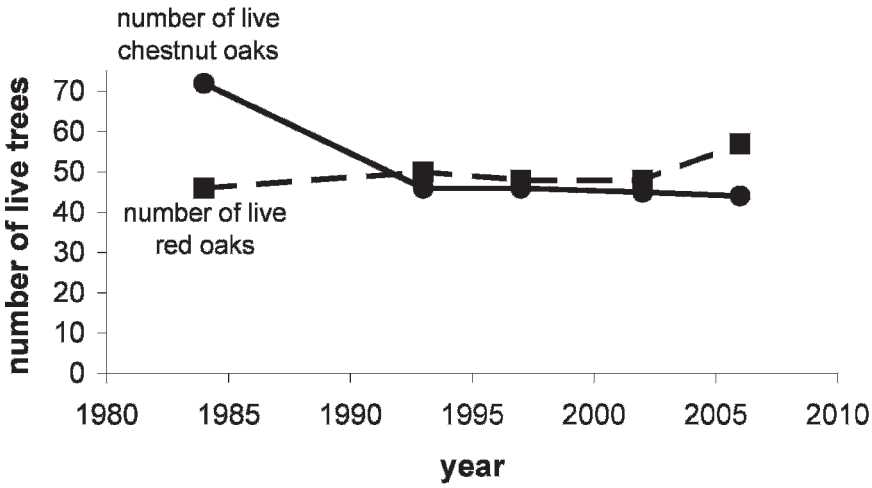

FIG. 1. Changes in the total number of live *Quercus prinus* and *Quercus rubra* trees from1984–2006 in the subset of 19 plots for which canopy censuses were conducted in 1993, 1997, and 2002. Canopy census data were provided by Julie Hart (unpublished data).

There were significant differences in tree species composition between the two land use history types in both 1984 and 2006. In 1984, post-agricultural plots had higher densities of *Betula lenta* and *Fraxinus americana* whereas former woodlot plots had higher densities of *Quercus prinus*. In 2006 there were higher densities of *Acer rubrum* L. (red maple) and *Fraxinus americana* in post-agricultural plots and higher densities of *Q. prinus* in former woodlots (Table 2). We also found that post-agricultural plots increased significantly in biomass and basal area between 1984 and 2006 but former woodlot plots did not (Table 3).

SAPLINGS AND SEEDLINGS. The total number of saplings were similar in the two censuses (1877 saplings in 1984 and 1907 saplings in 2006; saplings per ha are given in Table 4). Size distributions for saplings were also very similar in 1984 and 2006. Notable significant trends in sapling density include an increase in *Betula lenta* by 560% and declines in *Acer rubrum* by 54%, *Pinus strobus* L. (white pine) by 80%, *Quercus rubra* by 89%, and *Tsuga canadensis* by 88%. Seedling density in 2006 was roughly twice as high as in 1984, with a total of 1473 seedlings (85640 seedlings ha^{-1}) in 2006 versus a total of 717 seedlings (41690 seedlings ha^{-1}) in 1984. Other statistically

Table 2. Correlations between land use history and adult tree density in 1984 and 2006. Differences between land use history categories within a year were calculated using unpaired *t*-tests and significance is denoted by * = $P < 0.05$ or ** = $P < 0.01$. Differences between years within a land use category were calculated using paired *t*-tests and significance is denoted by † = $P < 0.05$ or † † †= $P < 0.001$. All data are given in number of stems ha^{-1}.

Species	1984		2006	
	Post-agricultural plots	Woodlot plots	Post-agricultural plots	Woodlot plots
Acer rubrum	124	44 †	83 *	27*†
Acer saccharum	35	61	47	85
Betula lenta	32	20	34	17
Carya glabra	53	34	40	27
Fraxinus americana	26*	7*	24*	4*
Pinus strobus	72	28	51	34
Quercus alba	8	19	7	14
Quercus prinus	40**	124**†††	30*	75*†††
Quercus rubra	40	51	39	65
Tsuga canadensis	42	80	42	96
All trees	579†	497	449†	489

Table 3. Land use history effects on mature tree biomass and basal area. Basal area was measured in m^2 ha^{-1}, biomass was measured in g m^2, basal area increment was measured in m^2 ha y^{-1} and biomass increment was measured in g m^2 y^{-1}. Biomass and basal area increased significantly in post-agricultural plots; significance of $P < 0.01$ is denoted by **.

	1984		2006		Basal area increment	Biomass increment
	Basal area	Biomass	Basal area	Biomass		
Post-agricultural plots	25.0	13,820	27.6**	17,160**	0.127	152
Woodlot plots	25.5	16,750	27.7	18,590	0.109	83.6

significant trends include an increase in the seedling densities of *A. saccharum* by 656%, *Q. rubra* by 216%, and *Q. prinus* by 1050%. In general, changes in associations of saplings and seedlings with land use history types reflected the patterns observed for the mature trees, but the differences between land-use history types were not statistically significant (data not shown).

Herbaceous Species. A total of 50 herbaceous species were present in 1984 compared to 39 in 2006. There was no significant difference in total herbaceous cover between the two time periods (4.75% in 1984 vs. 4.89% in 2006). Although many changes in the occurrence and percent cover of various herbaceous species were found, only the largest or most interesting are reported (Table 5). The invasive species *Alliaria petiolata* M. Bieb. (garlic mustard) increased significantly in percent cover from 0.21% of the forest floor in 1984 to 1.01% in 2006 ($P < 0.05$), making it the most abundant herbaceous species in 2006. Its frequency of occurrence also increased significantly from 6 quadrats in 1984 to 30 in 2006 ($P < 0.05$); these quadrats were in a total of 1 plot in 1984 and 10 in 2006.

Shrubs. Total shrub cover declined slightly over the course of the study, from 9.77% in 1984 to 7.90% in 2006, although this difference was not significant. The most prominent shrubs were *Viburnum acerifolium* L., *Cornus racemosa* Lam., *Vaccinium spp.*, and *Parthenocissus quinquefolia* L. Planchon. *V. acerifolium* decreased 37% in cover between 1984 and 2006 ($P < 0.05$). *Toxicodendron radicans* L., and members of the *Rubus* genus increased in cover, as did the invasive shrubs *Euonymus alatus* (Thunb.) Siebold and *Lonicera tatarica* L., but these increases were not statistically significant.

We also found that more invasive shrubs, including *Berberis thunbergii*, *Euonymus alatus*, and *Lonicera tatarica*, were present in post-agricultural plots compared to former woodlots. This trend was particularly strong—all of the sampled cover of these three species in 2006

Table 4. Seedling density, sapling density, and sapling basal area per hectare for select tree species in 1984 and 2006. Seedling densities, reported in ha^{-1}, were measured in quadrats occupying a total area of 172 m^2; a single seedling extrapolates to a density of slightly less than 60 seedlings per hectare. Sapling densities are also reported in ha^{-1}. Sapling basal area is reported in m^2 ha^{-1}, and is highly weighted towards saplings in larger size classes. *P* is the probability that 2006 values are significantly different from 1984 values according to paired t-tests, where * = $P < 0.05$, ** = Differences $P < 0.01$ **, and *** = $P < 0.001$.

	Seedling density			Sapling density			Sapling basal area		
Species	1984	2006	*P*	1984	2006	*P*	1984	2006	*P*
Quercus prinus	1340	15410	**	16	27		0.0123	0.0132	
Quercus rubra	700	2210	*	35	5	*	0.0753	0.0039	*
Pinus strobus	60	60		15	3	***	0.0403	0.0154	
Acer rubrum	12210	19190		175	80	*	0.2271	0.1203	*
Tsuga canadensis	230	410		64	8	**	0.1845	0.0223	***
Acer saccharum	3200	24200	*	320	209		0.2309	0.2561	
Carya spp.	1100	1630		40	57		0.0568	0.0768	
Betula lenta	350	990		44	290	*	0.0280	0.1818	**
Quercus alba	1100	700		17	13		0.0235	0.0139	
Quercus velutina	290	930		16	20		0.0129	0.0126	
Fraxinus americana	7330	5230		70	46		0.0914	0.0182	**
All species	41690	85640	***	1743	1774		1.3879	1.3491	

Table 5. The frequency and percent cover of select herbaceous species in 1984 and 2006. Frequency refers to the number of quadrats in which the species occurred (out of the 344 sampled), and percent cover refers to the amount of the forest floor covered by that species. *P* is the probability that 2006 values are significantly different from 1984 values according to paired t-tests, where * = $P < 0.05$, ** = $P < 0.01$ **, and *** = $P < 0.001$.

Species	Frequency			Cover		
	1984	2006	*P*	1984	2006	*P*
Alliaria petiolata	6	30	***	0.210	1.010	*
Aralia nudicaulis	6	12		0.087	0.433	
Dennstaedtia punctilobula	0	8	**	0	0.616	*
Galium (genus)	19	9	*	0.099	0.035	*
Hepatica americana	9	0	**	0.030	0	*
Maianthemum canadense	47	89	***	0.404	0.314	
Pilea pumila	2	4		0.015	0.058	
Polygala paucifolia	5	2		0.038	0.006	
Potentilla (genus)	12	5		0.130	0.030	
Total herbaceous species	196	217		4.747	4.887	

occurred in five plots, all of which were post-agricultural. In contrast, there was significantly more *Viburnum acerifolium* in former woodlots. In fact, *V. acerifolium* was considered by Glitzenstein et al. (1990) to be one of the best indicator species for former woodlots.

SOILS. Average pH was 4.6 in 1984 and 4.68 in 2006 and the ranges in these two years were 4.0–5.5 and 4.23–5.08 respectively. Unfortunately, pH in 1984 was only measured to one decimal place which slightly obscured trends. Even so, pH increased at most sites, and the overall average increase of 0.1 pH unit was significant ($P < 0.05$). The largest decrease in plot pH was −0.6 and the largest increase was 0.8. pH increased the most at sites where it was the lowest in 1984 and decreased the most at sites where it was highest in 1984 (Fig. 2).

In most plots, the exchangeable Ca concentrations that we measured in 2006 from the archived 1984 soils were very similar to the original values for these soils reported by Glitzenstein et al. (1990). However, for the

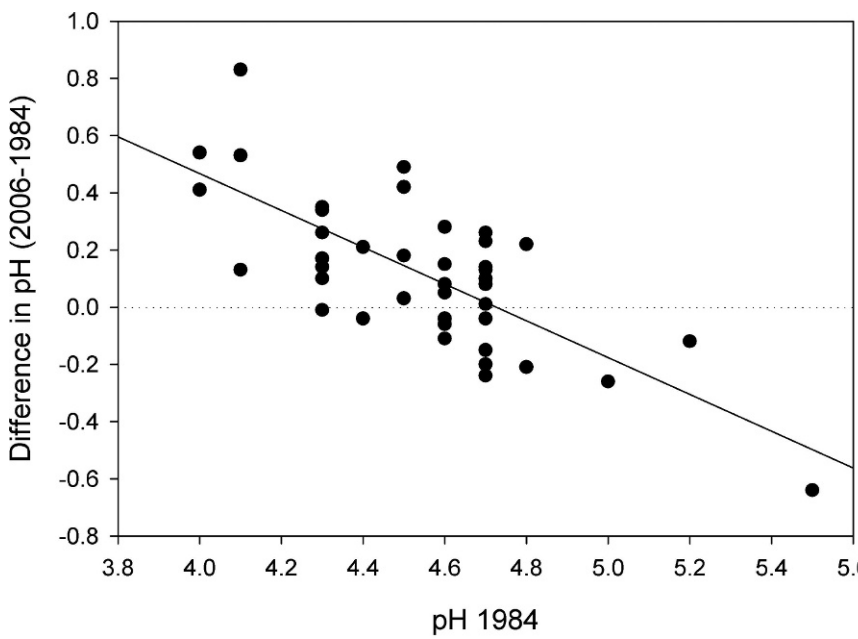

FIG. 2. The pH of each plot in 1984 and how it changed between 1984 and 2006. A positive difference in pH means that the pH was higher in 2006 than it was in 1984. The two variables were significantly correlated ($P < 0.0001$, $r^2 = 0.542$).

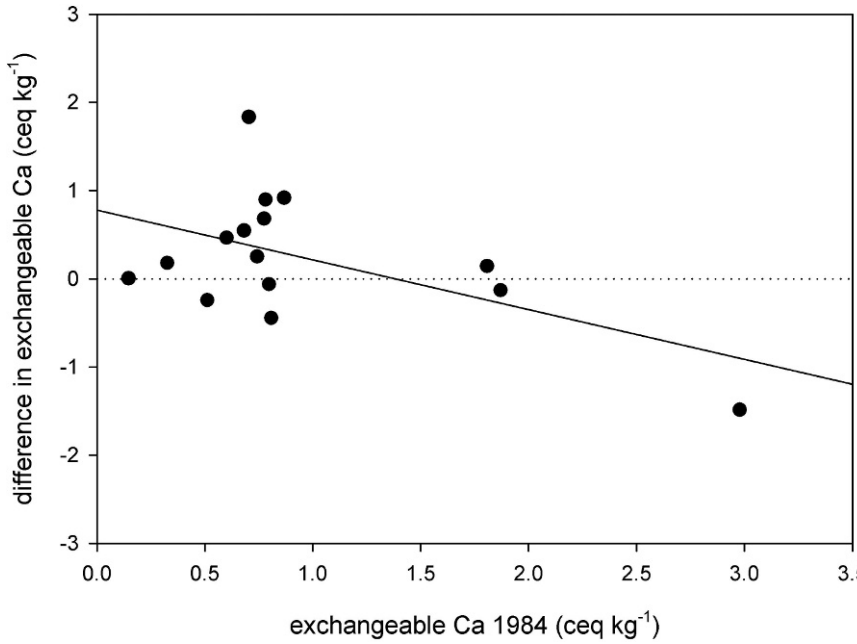

FIG. 3. Exchangeable Ca concentrations at each plot in 1984 and how it changed between 1984 and 2006. A positive difference in Ca means that the Ca concentration was higher in 2006 than it was in 1984. The two variables were significantly correlated ($P < 0.05$, $r^2 = 0.736$).

plots that had the highest levels of Ca, the measurements made on the archived soils in 2006 were much lower than the original values. The same pattern was found for Mg. Because the archived soils were stored dry in sealed bags, actual changes in Ca and Mg concentrations are unlikely, and we believe the differences may have been caused, in part, by analytical problems with the 1984 analysis. For this reason, we confine our analysis to the set of 17 plots for which we re-analyzed the archive samples, to ensure consistent analytical methods, instruments, and operators.

The mean exchangeable Ca concentration across the 17 plots was identical in 1984 and 2006 (mean = 1.63 ceq kg^{-1} dry soil in both years), but individual plots showed changes over time. Plots with the highest Ca concentration in 1984 lost the most Ca over the study period (Fig. 3), which is consistent with the patterns of change in pH (Fig. 2). Plots that had low concentrations of Ca showed less change. The same pattern also held true for exchangeable Mg (Fig. 4). No significant relationships were found between land use history and soil pH or base cation concentrations (data not shown).

Discussion. The correlations between land use and forest composition reflect both the effects of agriculture as well as farmers' preference for specific types of land (Glitzenstein et al. 1990). Many of the initial land use associations discovered in 1984 persisted into the present; *Quercus prinus* and *Fraxinus americana* continued to show significant associations with land use history. Although the association of *Betula lenta* with post-agricultural plots was no longer statistically significant, the general trend did not change. Likewise, although the association of *Acer rubrum* with post-agricultural plots became significant, the strength of the relationship remained similar. Two of the main species that were strongly associated with a particular land use history have diminished significantly (*A. rubrum* and *Q. prinus*), and two species that are less closely tied to the legacy of land use (*A. saccharum* and *Q. rubra*) have increased.

However, these forests are gradually becoming more similar because of both succession and disturbances (such as the decline in *Quercus prinus* due to gypsy moth defoliations, as discussed later). Post-agricultural plots declined significantly in tree density, to a point

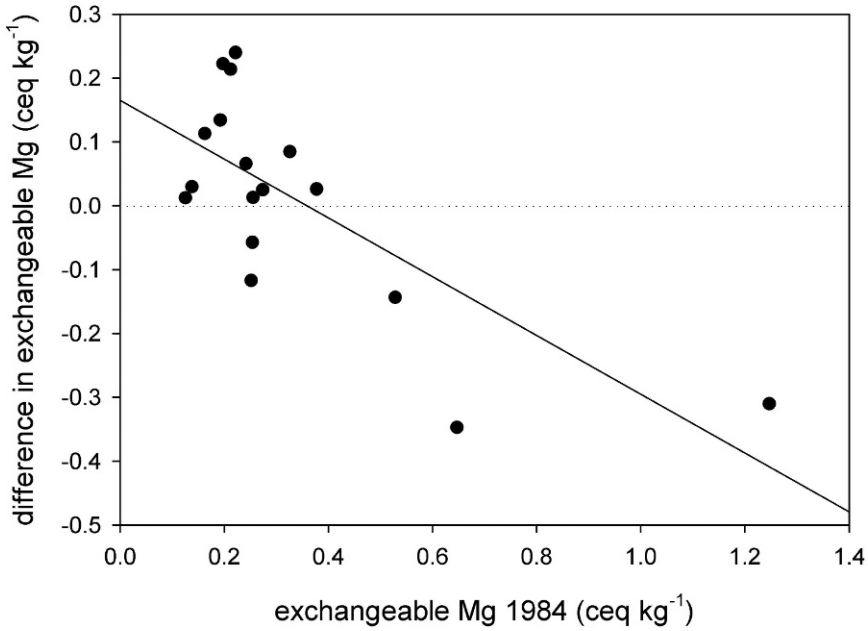

FIG. 4. Exchangeable Mg concentrations at each plot in 1984 and how it changed between 1984 and 2006. A positive difference in Mg means that the Mg concentration was higher in 2006 than it was in 1984. The two variables were significantly correlated ($P < 0.05$, $r^2 = 0.557$).

where they were comparable to woodland plots (see Table 2, final row). Other studies have found that tree density and size in post-agricultural areas generally recover to the point where they are comparable with less disturbed areas after roughly 100 years (Pallardy and Garrett 1998, Flinn and Marks 2007). Presumably, other differences in forest characteristics, such as light penetration, have also become more similar with time (Howard and Lee 2002, Flinn and Marks 2007).

Interestingly, the differences in tree biomass and basal area in forests with different land use histories also appears to have decreased over time. In 1984, biomass in the post-agricultural stands was lower than in the former woodlot stands, but by 2006 that difference had nearly disappeared, due to higher rates of biomass accumulation in the post-agricultural stands. Assuming tree biomass to be about 50% carbon, the carbon accumulation rate in biomass was low in these forests (mean of all plots = 63 gC m^2 y^{-1}) but it was over 80% higher in the post-agricultural stands (76 gC m^2 y^{-1}) compared to the former woodlot stands (42 gC m^2 y^{-1}). It is unclear if future trends in C accumulation rates in the two forest history types will be similar because their current biomass stocks are similar, or if they will continue to have different accumulation rates because their species composition is still quite distinct.

FOREST PESTS AND PATHOGENS. Most forest pests and pathogens are fairly host specific. If a tree species that is associated with a particular land use history is reduced in abundance by a pest or pathogen, it will reduce that legacy of land use history. The decline of *Quercus prinus* due to gypsy moth (discussed below) provides an example of this. However, if a tree species is not associated with a particular land use its decline will not affect correlations between land use histories and current species composition. The decline of *Cornus florida* due to a fungal pathogen offers an example of this.

The impact of many forests pests and pathogens is correlated with host tree density. This has been found for the hemlock woolly adelgid (Pontius et al. 2006) and beech bark disease (Griffin et al. 2003), and could have been causing some of the patterns in *Quercus prinus* mortality found in this study. If trees are more likely to be damaged in areas where the species is at higher densities, those tree species that have higher densities in areas with a particular type of land use will be dispro-

portionately affected by herbivory and disease in those areas. Agricultural abandonment also leads to forests that are relatively even-aged, which may increase susceptibility to pathogens (Smallidge et al. 1991). This could make forest pests and pathogens more likely to act as a force to reduce the legacies of land use history in these forests.

Chestnut Oaks and Gypsy Moth. The largest change in forest tree species composition over the study period was a decline in *Quercus prinus*, which decreased in density by 36% between 1984 and 2006 (Fig. 1). The decline in *Q. prinus* density and basal area occurred within a short period of time (1984–1993, as seen in Fig. 1). Of the 172 *Q. prinus* trees recorded in 1984, 46 were experiencing dieback, and there were an additional 21 standing dead trees. Records of gypsy moth populations at this site show very high population levels and severe defoliation in 1980–1981, and moderate populations and defoliation in 1989–1990 (Goodwin et al. 2005). It is probable that gypsy moths were the root cause of the mortality, and that many *Q. prinus* individuals succumbed after 1984 to stresses induced during 1980–81 (Campbell and Sloan 1977, Hennigar et al. 2007).

Generally, in co-occurring populations of *Quercus prinus* and *Q. rubra* the former is more heavily damaged by gypsy moth defoliation (Fajvan and Wood 1996, Muzika and Liebhold 1999) although exceptions do exist (Stalter and Serrao 1983). One factor may be that the larger bark ridges present on *Q. prinus* provide concealment for gypsy moth larvae, pupae and egg masses, lowering predation risk (Campbell et al. 1975). Another factor is that *Q. prinus* trees have foliage that is more nutritious (relative to *Q. rubra*) for gypsy moths (Kleiner and Montgomery 1994). Regardless of the mechanism, gypsy moth helped reduce the dominance of *Q. prinus*, which was strongly correlated with former woodlots. In doing so, it has partially obscured the correlation between 19th century land use and current forest composition. Moreover, gypsy moth defoliations disproportionately removed *Q. prinus* individuals in plots that had higher densities of these trees in 1984; *Q. prinus* declined by 25% in agricultural plots and by 40% in former woodlots. However, it is important to note that the correlation of *Q. prinus* with specific areas likely predated European colonization. Because these areas are generally steep and rocky they would have been less suitable for agriculture, and therefore more likely to have remained as woodlots (Glitzenstein et al. 1990).

This change in forest composition is also ecologically important, as the shift from *Quercus prinus* dominance has most likely induced shifts in other species of the forest food web as well. For example, *Q. rubra* acorns are dormant over the winter, whereas *Q. prinus* acorns germinate in the fall. These differences in acorn properties influence the population cycles of white-footed mice and other rodents (McShea 2000), which could potentially affect Lyme disease incidence (Ostfeld et al. 2006).

Flowering Dogwood. A significant decline in *Cornus florida* was observed over the 22 year interval. We assume that this was largely due to the fungal pathogen *Discula destructiva* (Heirs and Evans 1997), which has been causing dogwood mortality throughout the eastern U.S. (as summarized by Pierce et al. 2008) and first entered the Hudson River Valley in the early 1980s. Successional dynamics and shading by *Acer saccharum* could have been an additional factor (Pierce et al. 2008). It is likely that Glitzenstein et al.'s (1990) survey showed this decline in progress; in 1984 they recorded five live *C. florida* trees, of which four exhibited dieback. They also recorded an additional 12 standing dead *C. florida* trees. By 2006, only one live and one standing dead *C. florida* tree (> 10 cm DBH) were left. One hundred saplings were recorded in 1984 but only 10 were present in 2006, while seedling numbers declined from 35 to zero. Disturbingly, the low numbers of seedlings and saplings show little hope for any *C. florida* recovery within these forests in the near future. The loss of this sub-canopy tree species has undoubtedly affected the birds and small mammals that ate its fruits and may also affect the Ca cycling of the forest, because *C. florida* is known to "pump" Ca from lower horizons to the surface soil (Jenkins et al. 2007). However, because *C. florida* was not associated with any particular land use history, this decline does not alter any correlations with land use history.

Eastern Hemlock. This study recorded an overall increase in *Tsuga canadensis* tree density, relative density, basal area and relative basal area. Changes in *T. canadensis*

did not vary as a function of land use history. Indeed, the only two sites exhibiting large declines in the number of *T. canadensis* trees (plots 740 and 808) were both affected by an ice storm in 1987. *T. canadensis* is a late successional species, and its high shade tolerance could explain both the recruitment of new trees from saplings and high growth rates of already established *T. canadensis* trees in the Canoo Hills.

While this study has found that mature *Tsuga canadensis* trees are thriving in the Canoo Hills, its saplings and seedlings are not, even on north facing slopes. In 1984 there were 69 *T. canadensis* saplings recorded in 12 plots but in 2006 there were only 9 saplings in a total of four plots. Although some of this decrease in saplings is likely due to growth of saplings to trees (having attained a DBH > 10cm) most of this decrease is presumably due to a combination of sapling mortality and low rates of seedling recruitment. *Tsuga canadensis* seedling density was extremely low throughout the study period (with only four seedlings measured in all quadrats in 1984, and seven in 2006 (Table 2).

Tsuga canadensis trees in New England are threatened by two introduced pests, the hemlock woolly adelgid (*Adelges tsugae* Annand) and the elongate hemlock scale (*Fiorinia externa*) (Foster and Orwig 1998). The hemlock woolly adelgid is relatively new to the area, and from our observations there was no evidence of hemlock woolly adelgid induced mortality in the Canoo Hills at the time of our study in 2006. However, since the study was completed we have observed some adelgid-induced decline of hemlocks in parts of the study area, so this pest clearly has the potential to disturb *T. canadensis* populations in the future. Thus, although *T. canadensis* trees increased over the study period, limited recruitment and impending insect disturbances could extirpate this species. Because this species is primarily associated with woodlots and is rarely present in post-agricultural plots, loss of the species would reduce the difference between former woodlots and former agricultural plots.

INVASIVE PLANTS. Invasive plants are changing forest understory composition. One of the few herbaceous species to increase significantly was *Alliaria petiolata*, a notoriously invasive plant species. First introduced in the mid 1800s, the range of *A. petiolata* is expanding, and this species has invaded many habitats in the northeastern United States (Rodgers et al. 2008). As with many invasive species, *A. petiolata* outcompetes native vegetation, including both tree seedlings and herbaceous plants, and interferes chemically with mycorrhizal associations (Stinson et al. 2006, Stinson et al. 2007, Meekins and McCarthy 1999). While *A. petiolata* does exhibit some interannual variation in survival and growth (partly because it is drought sensitive; Meekins and McCarthy 2001), that is insufficient to explain this difference. It is likely that *A. petiolata* will continue to expand in the Canoo Hills, both geographically and in density, and could threaten certain native understory herbaceous plants. We did not find any correlations between the expansion of *A. petiolata* and land use history, so as the newly dominant herbaceous plant, this species has already obscured correlations between the composition of understory vegetation and the legacies of land use history. However, other studies have found correlations between land use and the abundance of invasive species (McDonald et al. 2008), leading us to the conclusion that the spread of invasive plants could either enhance or erode differences between forests with different land use histories, depending on the specific invasive and the site.

REGIONAL PATTERNS. The differences in land use history that we investigated are manifested on a scale of tens or hundreds of meters, and depend on land ownership and use patterns dating to the 19th and 20th centuries. However, many processes affect these forests on larger scales, transcending these boundaries. If these larger-scale phenomena affect forests both with and without agricultural histories, they can reduce overall differences between land use types.

One such large-scale trend is the establishment of an *Acer* understory in *Quercus*-dominated forests, which has been observed by many researchers in recent decades (Lorimer 1984, Abrams 1998). In many cases, this *Acer* understory has begun to replace *Quercus* trees in the canopy (McDonald et al. 2003, Dodge 1997, Drury and Runkle 2006, Galbraith and Martin 2005). While *Acer rubrum* has been observed in this role the most frequently (Lorimer 1984, Abrams 1998), it is not uncommon for *A. saccharum* to play a similar role (Pallardy et al. 1988, Runkle et al.

2005, Ozier et al. 2006). Deer provide a strong selection pressure on seedlings in the region, and could be influencing which species of *Acer* is more successful in the understory (Long et al. 2007). Researchers have shown that while there are a variety of other factors contributing to a lack of *Quercus* regeneration (Bruhn et al. 2000, Sork 1984) it is primarily associated with long term fire suppression and a lack of other disturbances, as *Quercus* species are out competed under their own canopies by more shade tolerant species in all but the most drought prone and low nutrient sites (Abrams and Nowacki 1992, Canham et al. 1994, Abrams 2003, McDonald et al. 2003, Iverson et al. 2008, Nowacki and Abrams 2008). This is a regional pattern, and seems to be a result of how management practices affect successional dynamics; this phenomenon occurs in areas regardless of land use history. Gypsy moth defoliations and subsequent oak mortality have hastened this process in other forests (Fajvan and Wood 1996, Jedlicka et al. 2004), and are probably doing the same in this forest. While it is likely that *Quercus* species will continue to dominate the forest canopy of the Canoo Hills in the foreseeable future, the increasing numbers of *A. saccharum* in the sub canopy are already reducing the legacies of land use history by establishing in both former woodlot plots and former agricultural areas. Similar results have been reported in Ohio (Drury and Runkle 2006).

Soil Chemistry. Changes in soil pH from 1984–2006 were statistically significant but small (mean change = + 0.1 pH unit) and are thus difficult to interpret. The plots with the highest pH in 1984 tended to decrease in pH, while those with lower pH in 1984 tended to remain constant or increase. Although trends in soil exchangeable Ca and Mg concentrations were based on fewer samples (only those archived 1984 soils which could be re-analyzed in 2006), a similar pattern was observed—the plots with the highest 1984 concentrations decreased the most. Thus, soil characteristics seem to have homogenized over the study period. The decline in base cation concentrations and pH in the better-buffered plots could be caused by leaching of Ca, which results in part from the acid deposition which affects this area (Kelly et al. 2002, Lovett and Hart 2005). Although other researchers have found that changes in soil chemistry can be caused by shifts in forest composition (Jenkins et al. 2007), differences in pH, Mg, and Ca in this study were not correlated with changes in tree density or basal area of *Acer saccharum*, *Cornus florida* (including saplings), or *Tsuga canadensis*. Because acid deposition is a regional factor it will affect plots regardless of their land use history. While we did not find any correlations between land use history and pH or base cation concentrations, others have found differences such as reduced levels of soil organic matter, carbon, phosphorus, and spatial heterogeneity in post-agricultural forests (Flinn and Marks 2007). However, a study in a similar forest found that these slight differences in soil chemistry are not likely to perpetuate differences in plant community composition (Matlack 2009).

We did observe that the plots with the largest loss in Ca also had the largest decline in *Acer saccharum* saplings ($r^2 = 0.57$, $P < 0.05$, $n = 16$ plots). We do not believe that this correlation is caused by a reduction of *A. saccharum* influence on soil Ca due to the loss of saplings, because the saplings likely contribute only a small fraction of the biomass and litter production of the plot. However, the survival of *A. saccharum* saplings is known to be sensitive to Ca availability (Kobe et al. 1995), thus we suspect that the Ca loss may have contributed to the decline of the saplings. Because Ca loss from the soils is associated with sulfur deposition at this site (Lovett and Hart 2005), it appears that acid deposition may be negatively influencing *A. saccharum* regeneration. However, only two of the 16 plots showed both high loss of Ca and a large decline in *A. saccharum* saplings, so more sampling would be necessary to confirm this hypothesis.

Future Trajectory of Forest Composition. This study has documented many shifts in forest composition in the Canoo Hills during the period of 1984 to 2006. Similar changes in forest composition have been documented in other forests over this period (Galbraith and Martin 2005). Some of the changes appear to reflect maturation of the forest due to succession, such as the increase in the shade tolerant trees *Acer saccharum* and *Tsuga canadensis*. Others are due to external drivers, such as the pathogens and pests which appear to have caused the declines in *Cornus florida* and *Quercus prinus*. Significant changes

in species composition such as those reported here can have substantial effects on forest ecosystem processes, understory vegetation and on the forest food web. The combination of internal successional properties and externally applied stresses has influenced the trajectory of this forest over the past 22 years, and these processes will presumably continue to dictate the path of this forest in the future.

While many of these changes are large and reflect changes in ecologically important species, it is important to note that the forests of New England are historically both dynamic and resilient, and that the rise or decline of individual species has been a regular occurrence in these forests. For example, *Castanea dentata* Marsh. (American chestnut) was not a major forest species until about 1,500 years ago, when changing climactic conditions shifted forest composition (Foster and Aber 2004). After *C. dentata* was eliminated by chestnut blight (caused by *Cryphonectria parasitica*) in the early 1900s, forests recovered with altered species composition (Keever 1953). Moreover, *Tsuga canadensis*, which was almost completely eliminated about 5,000 years ago, recovered to become one of the most important tree species in the Northeast (Foster and Aber 2004).

However, how the forest will react to new pests and pathogens is unknown. The devastation of *Cornus florida*, the lack of *Tsuga canadensis* recruitment, and the host of threatening insects and pathogens could combine to cause serious changes in Northeastern forests. The spread and severity of these various pathogens is uncertain, but there exists a strong potential for more shifts in forest composition in the immediate future. It is also likely that other species-specific pathogens will eventually reach this forest; the emerald ash borer (*Agrilus planipennis* Fairmaire) is very likely to infest this area in the near future which would reduce differences in forest composition between former woodlots and agricultural areas. The Asian long horned beetle (*Anoplophora glabripennis*) and sudden oak death (caused by *Phytophthora ramorum*) may threaten these forests in the longer term. All three have the potential to cause extensive mortality with numerous ramifications for the ecosystem (Lovett et al. 2006). All of these predictions of the future composition of the forest are highly uncertain, but the large changes in forest composition that result are likely to overshadow many of the legacies of land use history.

CONCLUSION. In summary, we have found that the legacies of land use history are still readily apparent in species composition. Regional patterns are playing important roles in shaping successional trajectories and gradually reducing the signs of past land use, as can be seen in the example of *Acer* dominated understories. However, species-specific disturbances, such as the decline in *Quercus prinus* due to gypsy moth, have also played an important role, and novel pests and pathogens can be expected to do so even more in the future. Our work implies that although many of the legacies of land use history can persist for long periods of time in a relatively stable forest, novel species-specific disturbances associated with global change may overwhelm the traces of previous land use.

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